OBSERVATIONS ON *ASCOSCHÖNGASTIA INDICA* (HIRST 1915) (ACARINIDA: TROMBICULIDAE)

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INTRODUCTION

U. S. Naval Medical Research Unit No. 2 was established in such a way that specialists of all types that might be useful in attacking medical problems that concerned the Navy in the Pacific area were included on its roster. The author was included in the unit as an acarologist. In the Pacific area the acarological problem of most importance to naval medicine is concerned with mites of the family Trombiculidae. Larval mites, chiggers, of this family are known to transmit tsutsugamushi fever to man in many parts of the Pacific area (Wharton in press). Medical research on the disease has been hampered by the inability of investigators to culture trombiculids by controlled and precise methods. The facilities afforded by Namru 2 were ideal for a study of the life-history of trombiculid mites.

Tsutsugamushi disease does not occur on Guam where Namru 2 is located. However it was felt that the fundamental work in development of techniques for culturing mites, and ecological studies of mites in the field would apply with minor variations to the vectors of tsutsugamushi disease. Furthermore the danger of becoming infected with the disease was eliminated in this way, and the elaborate precautions necessary to experimentation with typhus could be eliminated from routine work. The author has investigated three areas where tsutsugamushi disease is endemic and observations made on *Trombicula deliensis,* a vector of the disease, are consistent with the assumption made above.

The most readily available species of trombiculid mite on Guam is *Ascoschöngastia indica,* a parasite of rats. This species was chosen as a subject for investigation because in addition to its ready availability it was the only one of ten species of trombiculids on Guam whose habits approximated, those of vectors of the disease. The present study presents information obtained from observations and culture experiments from May 1945 through December 1945.

This report is the result of the combined efforts of members of the laboratory of acarology. R. K. Carver, PhM 2/c and J. N. Strong who were in charge of the culture room during the time covered by this report, deserve much of the credit. J. M. Fritts, PhM 1/c, R. E. Muhl, PhM 3/c and others helped with the field work. The cooperation of the laboratories of entomology and mammalogy is also acknowledged, especially that given by Lt. Comdr. D. H. Johnson, who identified the mammals, and Lt. R. H. Baker, who identified the birds, both of mammalogy and Comdr. H. S. Hurlbut of entomology. The interest and encouragement of Commodore T. M. Rivers, Medical Officer in Command, are appreciated. The work of compiling data and preparing manuscript was done at the U. S. National Museum under the command of Rear Admiral H. W. Smith. His cooperation and that of his staff, especially Lt. Comdr. Mildred R. Lewis, are gratefully acknowledged. Identifications of organisms associated with *Ascoschöngastia indica* were made by specialists in the U. S. National Museum and credit for the determinations is given in the appropriate places. Mr. C. F. W. Muesebeck, Chief of the Division of Insect Identification, U. S. Department of Agriculture, Dr. H. E. Ewing, retired, Dr. E. W. Baker, Acarologist, U. S. Department of Agriculture and Dr. E. A. Chapin, Curator of Insects of the U. S. National Museum were particularly helpful.

REVIEW OF LITERATURE

Hirst 1915 described *Schöngastia indica* as a new species from Calcutta, India. The bandicoot then known as *Nesokia (Gunomys) bengalensis* but currently as *Bandicota bengalensis* was reported as the host. Hirst's description is satisfactory for the identification of the species. Walch 1922 described *Trombicula muris* from a rat at Deli, Sumatra. His description of this species shows it to be the same as *Schöngastia indica.* In 1924 Walch described the nymph of *S. indica* but unfortunately figured the sensillae incorrectly. Walch in 1927 recognized the synonomy of *T. muris* with *S. indica.* At this time he also reported it on rats from southern Sumatra and Macassar, Celebes. Fletcher, Lesslar, & Lewthwaite 1928 reported *T. muris* on rats in Malaya. Ewing 1929 erected the genus *Neoschöngastia* for species of *Schöngastia* that lacked a row of dorsal cheliceral teeth. Gater 1932 places *S. indica* in Neoschöngastia. Gater recorded the species from the Federated Malay States on *Rattus rattus, Rattus concolor, Rattus sabanus,* and *Rattus canus.* He reported that *N. indica* was widespread and occurred in both town and country. In 1940 Heaslip found *N. indica* on rats from Cairns, Queensland (Womersley & Heaslip 1943). Gunther 1941 reviewed the records of *N. indica* from the Dutch East Indies. Radford 1942 included *N. indica* in his review of the Trombiculidae. Womersley and Heaslip 1943 reported a specimen of *N. indica* from Batavia, Java. Ewing 1946 pointed out that Womersley 1940 divided the genus Neoschöngastia properly but that he unfortunately applied the new name Paraschöngastia to the group that contained the type of the genus Neoschöngastia. Therefore Ewing proposed the generic name Ascoschöngastia for the group that includes the species under discussion and its present name is *Ascoschöngastia indica* (Hirst 1915) (new

combination). Radford 1946 reports certain features of the life history and biology of *Ascoschöngastia indica* from Ceylon and the Maldive Islands. At Colombo and Embeliptiya, Ceylon it was found in the ears of *Rattus rattus* while at Addu Atoll in the Maldive Islands the host was *Rattus norvegicus*. In all 194 nymphs of *A. indica* were reared in the laboratory. Engorged larvae were placed in vials that contained a mixture of moist sand and ground leaves. In from six to eight days nymphs were found in these vials. Attempts to rear adults from nymphs failed. In the soil-like debris found in the tops of coconut trees, adults of *A. indica* were found. Radford describes certain features of the morphology of *A. indica* very briefly. He correctly describes the sensillae of the nymph that were incorrectly interpreted by Walch. His figures of *A. indica* are diagrammatic and while they present the more general features, they frequently do not correspond in detail with the specimens. For example, his figure of the adult of *A. indica* shows numerous setae on what appear to be the basal segments of the chelicerae when in reality no setae occur on the basal segments of the chelicerae in any of the Trombiculidae. The above discussion of Radford's figures is offered not in criticism of his valuable contribution, but as a guide to future workers who may be tempted to extract more information from the figures than they were intended to provide. Wharton & Carver (in press) discuss briefly the food of *A. indica*. Philip and Woodward report *A. indica* from several localities on Luzon, Philippine Islands. They found it in the ears of several small rodents including *Rattus mindanensis*.

In addition to literature on *A. indica* papers concerned with life histories and biology of other species of trombiculids are also pertinent to the present study. *Trombicula akamushi* has been well studied by Japanese investigators. All stages in its life history have been described or figured. The genital apertures in the adults however have not yet been presented in such a way that males and females can be differentiated. Miyajima & Okumura 1917 report seven stages in the life history: egg, deutovum, larva, nymphochrysalis, nymph, imagochrysalis, and adult. According to them eggs are probably laid singly in the soil, during development the eggshell splits sometime before the hatching of the six-legged larva. The larvae or chiggers attach to small mammals and after feeding for three or four days free themselves and seek shelter in the soil. A nymphochrysalis develops from which the nymph emerges in five or six days. The nymphs are reported to feed on potatoes, melons, and other vegetables but not on acid fruits such as oranges and apples. After ten weeks a few nymphs will become adults. No mention of the imagochrysalis is made in the text but a figure of the imagochrysalis is given.

Ewing 1944 summarizes the knowledge available for the common American chigger *Eutrombicula alfreddugèsi*. Only the larva, nymph, and adult of this species are known, but the sclerotized genital structures of the males and females have been described. Little information is available on the habits of *E. alfreddugèsi* except for the host preferences of the larvae. Adults of *E. alfreddugèsi* have been collected from humus.

Although much work has been expended on the life history of the common European chigger *Trombicula autumnalis* the adults have not yet been reared. André 1930 reports rearing of nymphs and describes an adult that is so similar to the reared nymph that there is little doubt that it is the adult of *T. autumnalis*. The behavior of free-living larvae of *T. autumnalis* has been studied by André 1938. He discovered their remarkable habit of congregating in great masses during certain periods of the day. Keay 1937 in a paper on the ecology of *T. autumnalis* gives a detailed account of its distribution in the British Isles and emphasizes the discontinuous distribution of this species.

Michener 1946 describes the life history of a Central American chigger in detail. His valuable paper presents the most complete account of the life history of any chigger that has yet appeared. The egg, deutovum, larva, nymphochrysalis, nymph, imagochrysalis, and imago are described and figured. He reports that eggs are laid singly on the ground. In four or five days the eggshell splits and a deutovum is revealed. Six or seven days later the larva emerges from the deutovum. Larvae engorge on chickens for from two to ten days after which they detach and become quiescent. A nymphochrysalis (protonymph of Michener) is formed within the larval skin. In from five to seven days nymphs emerge that become quiescent in from sixteen to forty-nine days. Within the nymphal skin an imagochrysalis (preadult of Michener) develops. Five to seven days later the imago or adult emerges and lives up to forty-five days under laboratory conditions. Michener's culture methods are described. He uses fruit jars with open tops for containers, plaster of Paris to control the humidity, and chicken dung mixed with soil as food. His culture methods were adapted from those used by Melvin 1946 who worked at the same laboratory. Melvin reports that eggs are laid in clusters rather than singly and also records carrying mites through two or more generations. Melvin is the first worker to achieve this. Both Melvin and Michener were working with a species recently discussed by Ewing 1946 under the name *Acariscus hominis*. Melvin calls the species *Eutrombicula hominis* while Michener refers to it as *Eutrombicula batatas*. Michener may be correct in his synonomy but the evidence he presents is not conclusive since he did not have topotypical material of *A. batatas* for comparison with *A. hominis*.

The biology of other species is even more incompletely known than that of those discussed above. Nymphs of several species have been reared, and the eggs of one species *Guntherana kallipygos* were found by Gunther 1939 on the hairs of the host that

is parasitized by larvae of *G. kallipygos*. Nymphs and adults of this species are still unknown. The presence of eggs on the host is unusual and is considered to be a very specialized type of behavior.

Ewing 1926 succeeded in rearing nymphs and adults of *Hannemania hylae*. The genus Hannemania does not belong in the family Trombiculidae but is a member of the closely related family Leeuwenhoekidae. Its life history is very similar to those that are known for trombiculids. Only the active stages: larva, nymph, and adult were described. No definite information concerning the food of nymphs and adults was obtained. The biology of a more distantly related mite that belongs to the Trombidiidae has been studied by Severin 1944. He found it to have the same stages as a trombiculid mite and also discovered that the nymphs and adults fed on the eggs of grasshoppers.

MORPHOLOGY

The morphology of *A. indica* has not been studied except superficially. In fact the exact morphology of so few trombiculids is known in all of the stages of the life history that Ewing 1944 in discussing future work on the Trombiculidae states "The need for a thorough morphological study of at least one economically important species of the Trombiculidae is apparent." Unfortunately the present discussion must be limited to the sclerotized structures of the cuticle and its derivatives since no preparations that will show the soft structures have been made. It may appear that description of each type of seta and the location of the setae on the larvae and certain structures in the nymphs and adults is too detailed, but experience shows that these structures are relatively constant within any species. Particular attention is given to the internal skeletal structures of the gnathosoma and genitalia because these have been ignored by other workers. Wharton 1938 and Ewing 1944 figure the genital armature of trombiculids in some detail.

Egg (Fig. 1)—The freshly laid egg of *A. indica* is a sphere with a diameter of 150 microns. Its external shell or chorion is covered with raised, irregular, blister-like ridges that are arranged in irregular fashion over the entire surface. During production of eggs within adult females several partially developed eggs may be seen at one time, but only one or two eggs show the completed shell.

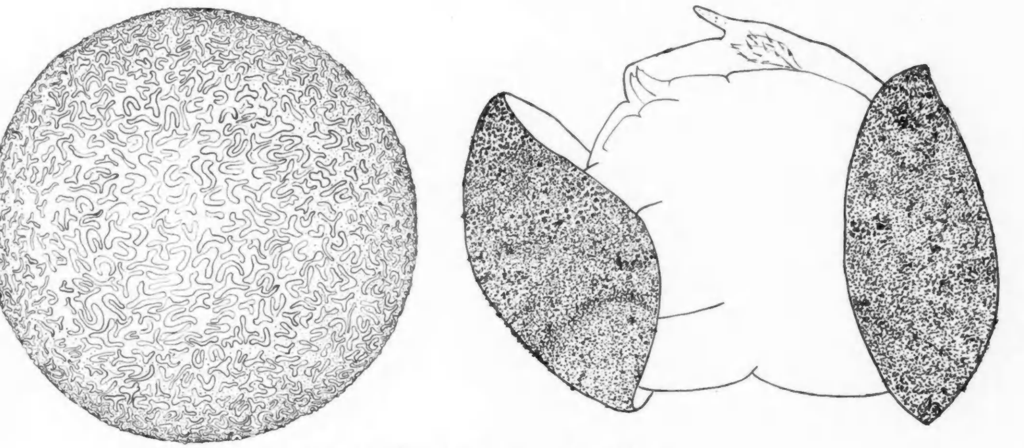

FIG. 1. Egg and deutovum of *A. indica*.

Deutovum (Fig. 1)—During development the ornamented shell splits and the growing larva is then enclosed by a thin granular membrane, the secondary cuticle, that is formed within the shell. This stage is known as the deutovum. The deutovum is 182 microns long. The pseudostigmatic organs of the developing larva project into the deutoval horn. The larval gnathosoma and legs differentiate in expanded portions of the deutovum. The palps are folded ventrally, but the legs are directed anteriorly. It is characterized by a horn-like projection similar to that described below for the nymphochrysalis.

Larva (Figs. 2-6)—Unengorged larvae average 185 microns in length while those removed from rats averaged 309 microns and attained a maximum size of 394 microns. Larvae are orange white to cream in color except for the two pairs of eyes that are ruby red. The gnathosoma is joined to the idiosoma ventrally between coxae I. It is composed of the segments that bear the mouth parts and is frequently referred to as the capitulum. Dorsally the idiosoma or body extends over the proximal region of the basal cheliceral segments. The basal section of the gnathosoma is formed from the fusion of the maxillae, the coxae, and trochanters of the paired maxillary palps and the hypostome. Anterior to the fused palpal segments there are two pairs of maxillary lobes, a thin lamellar ventral pair, inner maxillary lobes of Ewing, that project well beyond the basal segments of the chelicerae but do not enfold them laterally

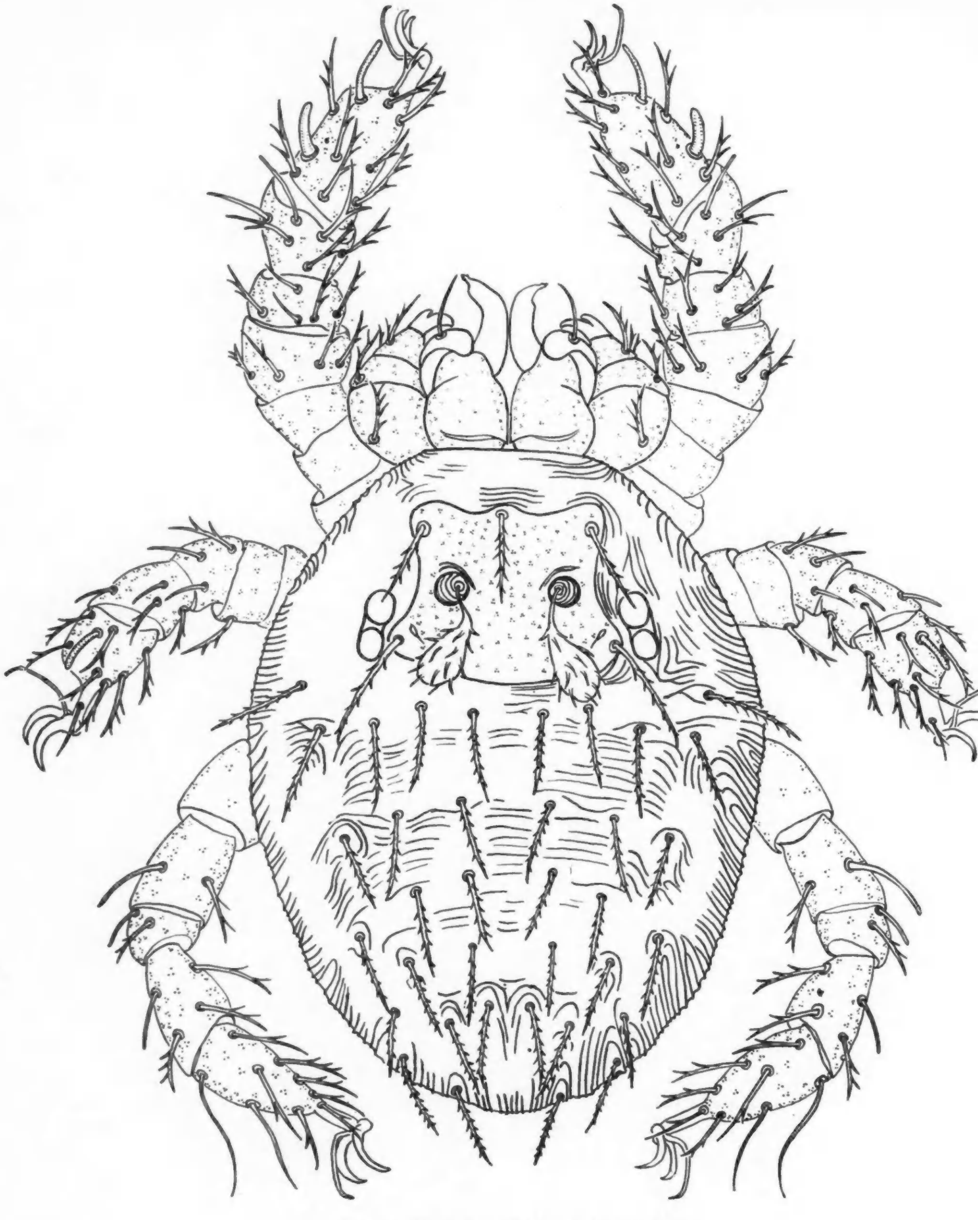

FIG. 2. Unengorged larva of *A. indica.*

and a heavier more dorsal pair the galeae, whose anterior lateral margins curl laterally and dorsally across the proximal portion of the distal cheliceral segments. A nude seta is situated on the dorsal anterior face of each galea just lateral to the chelicerae. On the first palpal segment which represents the fused coxa and trochanter is a plumose seta that has as many as eight long barbs. The seta is ventral since the first palpal segment is fused dorsally with the maxilla along most of its length and is free only at its distal margin. The palpal femur is expanded laterally. Its lateral margin is an even convex curve while the median margin is concave. Dorsally there is a feathered seta with as many as five medium-sized barbs. This seta is approximately equal in length to the segment which bears it. The palpal genu is

shaped like a short truncate cone. The base articulates with the femur. A seta with two fine barbs is situated dorsally on its proximal aspect. The palpal tibia articulates with the distal apex of the palpal genu. The tibial setae; dorsal, ventral, and lateral; are long, fine, and each bears one or two exceedingly fine barbs. Distally the tibia is armed with a stout bifid palpal claw whose length equals the length of the segment that bears it. Ventrally the palpal tibia articulates with the small palpal tarsus which opposes the tibial claw in thumb-like fashion. The palpal tarsus bears dorsally a single large plumose seta with four pairs of barbs. Apically there are two plumose and a single nude seta. On each side midway between the distal and proximal limits there is a single plumose seta. Ventrally near the proximal margin there is a striated sensory seta that is shorter than the palpal tarsus. The chelicerae (Fig. 3) are composed of two segments. The basal segment is bulbous and has a dorsal transverse suture proximally.

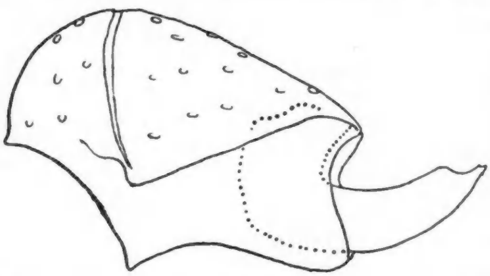

FIG. 3. Medial view of chelicera of a larval *A. indica.*

Distally the basal segment accommodates the expanded, greatly enlarged base of the chitinous distal segment. The chitinous distal segment curves dorsally from its base to terminate in a needle-sharp apex. Proximal to the dorsal tooth the segment increases in depth so that there is a sharp elevation in its dorsal margin. Within the body of the gnathosoma are two paired skeletal structures. The lateral elements represent the sunken coxae of the maxillary palps as is evidenced by their shape and position. The medial tube-like structures are in the position of the tracheal system of later stages of related mites and probably represent the sclerotized trunks of the respiratory system. (Fig. 4.) The mouth is closed by three pointed lips and lies ventral to the chelicerae in the midline at a level halfway between the proximal and distal margins of their basal segments.

Leg I is composed of seven segments. The coxa is triangular and contiguous with that of the second leg. It bears a single plumose seta which has a few fine barbs. At the posterior distal angle of the coxa there is a circular pit or urstigmen that is eight microns in diameter. The chitin about its margin is thickened and its walls are strengthened by a chitinous ring. It is five microns deep. The second segment, trochanter, is wider than long and bears a long plumose seta on its anterior ventral surface. The

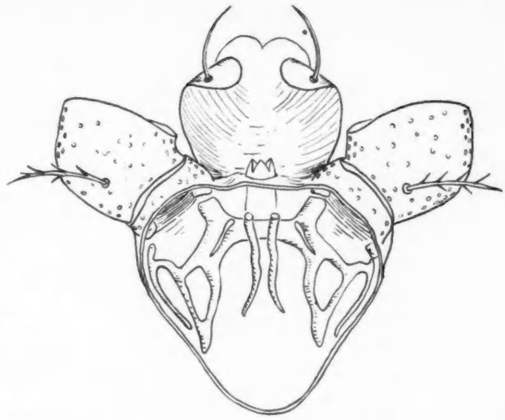

FIG. 4. Gnathosoma of larval *A. indica* with the chelicerae and idiosoma removed to show the mouth, and sclerotized structures that probably represent palpal coxae and tracheal trunks.

femur is divided into basifemur and telofemur. A single plumose seta arises from the posterior dorsal margin of the basifemur. The telofemur bears a ring of five plumose setae about its middle. The genu or fifth segment bears a ring of four plumose setae, three nude striated sensory setae of slender proportions and a single micro-sensory seta between the distal striated sensory setae. There are eight plumose setae on the tibia as well as a pair of slim striated sensory setae that flank a micro-sensory seta. The terminal leg segment or tarsus bears nine proximal plumose setae, twelve more distal plumose setae, one stout striated sensory seta, one slim striated sensory seta with a basal collar, and one micro-sensory seta. (Fig. 5) Leg II is composed of seven segments. The coxa bears a single long seta that appears nude but may have a few fine barbs. There is a single long plumose seta on the ventral anterior side of the trochanter. The basifemur carries two plumose setae one dorsal and one ventral. Four plumose setae are on the telofemur arranged in a transverse line across its dorsal surface. The genu has three plumose setae and a single slim striated sensory seta. The tibia has six plumose setae and two slim striated sensory setae. The tarsus has fifteen plumose setae, two striated sensory setae, one of which is fairly stout while the other is slim and a single micro-sensory seta. Leg III is also composed of seven segments. The coxa is not contiguous with coxa II and bears a single, long, apparently nude seta which occasionally has a few fine barbs. There is a single plumose seta on the trochanter. The basifemur has a pair of plumose setae, one dorsal the other ventral. Three plumose setae are situated on the dorsal aspect of the telofemur. Three plumose and one slim striated sensory setae were found on the genu. The tibia bears six plumose setae and a single slim striated sensory seta. On the tarsus there are two

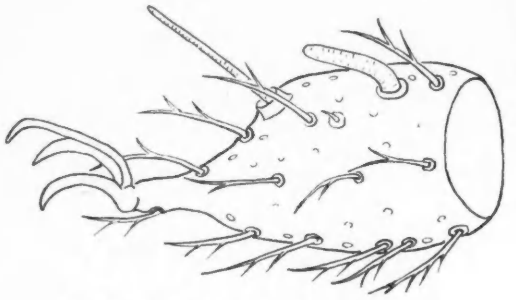

FIG. 5. Tarsus of leg I of larval *A. indica*.

nude whip-like sensory setae and eleven plumose setae.

The tarsi of all legs bear a pair of long, strongly curved claws. Between the claws there is a longer and more slender claw-like empodium. The chitinous covering of the appendages is ornamented by scattered punctae.

The idiosoma or body is oval in shape and its cuticle is covered with fine striations. There is a dorsal plate or scutum on the propodosoma, the region of the body that bears the anterior two pairs of legs. Flanking the scutum is a pair of ocular plates in each of which is set two eyes arranged in tandem. The anterior eyes are larger and have more heavily sclerotized corneas than the posterior eyes. Posterior to the scutum there are about 38 plumose setae arranged in rows beginning 2-8-6-6- etc. The arrangement of the dorsal setae is not always constant. One of the more frequent variations seen in engorged specimens is the movement of a pair of setae from the second row to the first so that setal counts then run 4-6-6- etc. Variation in any of the rows is possible especially at the posterior end. On the ventral surface there is a pair of nude setae between coxae I, a second pair between coxae III, and a group of more posterior, shorter plumose setae arranged in rows approximately as follows: 6-6-6-6-2. The anus is flanked by the last row of setae. Table 1 gives setal counts of five specimens so that the variation can be more easily evaluated.

The scutum is lightly ornamented by fine punctae over its entire surface. It bears five plumose setae: an anterior-median, a pair of anterior-laterals, and a pair of posterior-laterals. There is a pair of enlarged pits of uncertain function, pseudostigmata, near the center of the scutum. From each pit there arises a clavate sensilla or pseudostigmatic organ. Its head is clothed with relatively large setules. Between the pseudostigmata and posterior lateral setae on each side is a slit-like scutal pore. Womersley and Heaslip 1943 have devised a system of standard data for describing the scutum. Nine measurements all in microns are used as follows:

AW = distance between the bases of the anterior lateral setae

PW = distance between the bases of the posterior lateral setae

SB = distance between the centers of the pseudostigmata

ASB = distance from the anterior margin to the pseudostigmata

PSB = distance from the posterior margin to the pseudostigmata

AP = distance between the base of the anterior-lateral seta and posterior-lateral seta

AM = length of the anterior median seta

AL = length of the anterior-lateral seta

PL = length of the posterior-lateral seta

S = length of sensilla or pseudostigmatic organ. (Figure 6.)

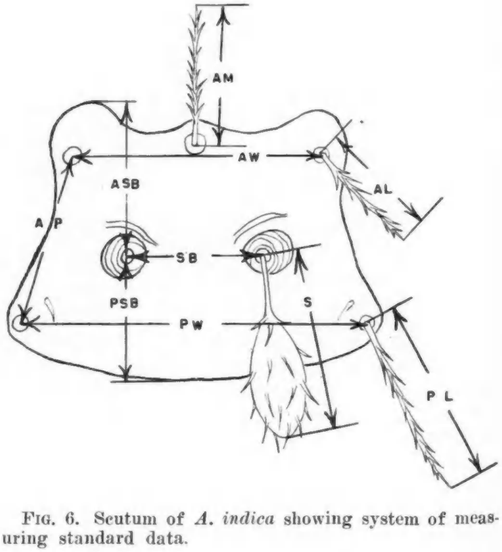

FIG. 6. Scutum of *A. indica* showing system of measuring standard data.

TABLE 1. Number of setae.

Row	Dorsal 1	2	3	4	5	6	7	8	Ventral 1	2	3	4	5	6	7	8	9	Total
Spec.																		
1	2	8	5	6	5	6	4	3	2	2	6	6	6	6	2	-	-	69
2	2	8	6	6	4	6	4	2	2	2	6	6	6	6	2	2	-	70
3	4	6	6	6	6	4	4	-	2	2	6	6	4	3	4	2	2	67
4	4	6	6	6	6	6	4	-	2	2	7	5	6	6	4	2	2	74
5	4	6	6	6	4	4	2	-	2	2	6	6	5	6	4	2	2	67

The mean of five specimens of *A. indica* from Guam: AW 36—PW 50—SB 20—ASB 21—PSB 18—AP 25—AM 22—AL 17—PL 29—S 27 (Table 2) compares favorably with the mean of four specimens from various localities measured by Womersley and Heaslip 1943: AW 36.5—PW 54—SB 20.5—ASB 18.5—PSB 17—AP 27—AM 23—AL 16—PL 30—S 26.

TABLE 2. Standard data of dorsal scutum. (in microns)

Spec.	AW	PW	SB	ASB	PSB	AP	AM	AL	PL	S
1	35	50	19	21	17	25	21	17	29	26
2	36	47	19	19	17	25	22	17	29	25
3	37	51	21	21	17	26	22	17	29	28
4	37	50	21	21	17	25	22	17	30	28
5	37	51	21	21	21	23	23	17	30	29
Mean	36	50	20	21	18	25	22	17	29	27

No indication of the genital opening is visible in the larva. The anal opening is at the posterior end on the ventral surface and is closed by a pair of crescent-shaped valves that are hinged laterally and swing outward when the uropore or anus is opened.

Nymphochrysalis (Fig. 7)—When engorged larvae prepare to undergo metamorphosis into the nymph they become quiescent. The muscles of the appendages undergo lysis and the material migrates to the body proper. The entire external surface of the larva breaks away from the cuticle and a thin layer of chitinous material is laid down within the body of the old larval skin. This stage is known as the nymphochrysalis. It is within this secondary cuticle that the nymph develops. The following description of the nymphochrysalis is based on a specimen that contains an almost completely developed nymph.

The old larval skin is stretched so that the striae so characteristic of the cuticle of the larva have disappeared. It measures 400 microns in length in the specimen shown in Figure 7. The gnathosoma, scutum, and two anterior pairs of legs remain in the position that they held in the engorged larva. Posterior to these structures elongation has taken place. The posterior pair of legs is widely separated from the second pair. In the mid-line just posterior to the scutum the larval skin is stretched out by the nymphochrysalis to form an anteriorly directed horn. The entire nymphochrysalis appears to be filled with fluid so that the developing nymph is immersed. The horn-shaped projection represents a weakened portion of the secondary cuticle of the nymphochrysalis. It is at this horn that the first break in the larval skin appears prior to the emergence of the nymph. The developing nymph can be seen inside of the secondary cuticle of the nymphochrysalis. It is oriented normally in relation to the larval skin that surrounds the nymphochrysalis. The gnathosoma of the nymph lies just below the scutum of the larval skin. The chelicerae project anteriorly and just reach the empty larval gnathosoma. The palps are folded ventrally and lie ventral to the gnathosoma of the developing nymph. The sensillae of the nymph project into the base of the anterior-median horn of the nymphochrysalis. The main body of the nymph is enclosed in the posterior dorsal portion of the larval skin. Ventrally the legs of the developing nymphochrysalis push the ventral portion of the larval skin out before them, so that each of the eight nymphal legs is enclosed in a "stocking." The anterior legs form an anterior-median pair of projections that originate at the level of leg two of the larva. The other three pairs of legs are progressively more posterior and lateral in position. All legs are directed backwards.

When examined under low magnification the nymphochrysalis appears to be in two layers. The fact that the main body of the nymph develops in the dorsal half of the larval skin while the legs develop in the ventral half is responsible for the characteristic appearance of the nymphochrysalis.

Nymph (Figs. 8-13)—Nymphs average 480 microns in length. They are salmon-white in color and have no eyes. The gnathosoma of the nymph is more elongated than that of the larva. The palpi of the nymph have six discrete segments in place of the five that are characteristic of the larva. The palpal coxae are fused with the maxillae as was the case with the larva but the trochanters are movably joined to the

FIG. 7. Nymphochrysalis of *A. indica* contained in larval skin. Nymph can be seen inside the nymphochrysalis.

coxae instead of fused with them. Sclerotized portions of the exoskeleton of the palpal coxae are submerged in the body of the gnathosoma and form an endoskeleton for it. The palpal trochanter is short, 14 microns, and narrow, 12 microns, in comparison with the femur. There are no setae on the trochanter.

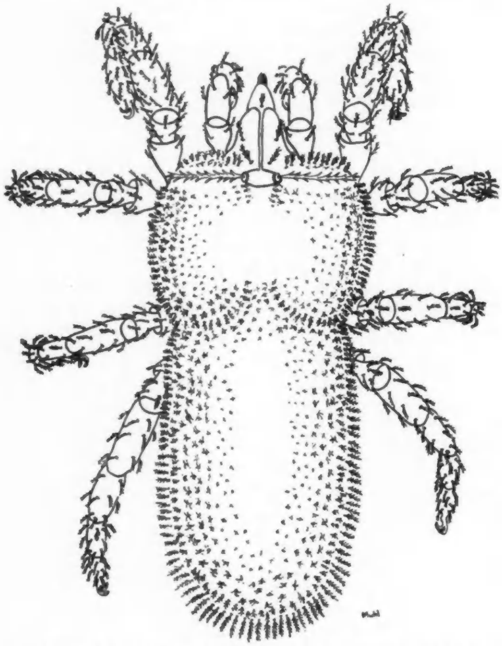

FIG. 8. Nymph of *A. indica*. (Drawing by Muhl.)

The expanded, 37 microns by 30 microns, femur bears three setae each having two or three barbs. The genu bears three similar setae. On the tibia there are three setae at the base similar to those on the preceding segments as well as two more distal plumose setae and two claw-like setae with blunt expanded tips at the base of the tibial claw on the medial side. The tibial claw is simple and curves ventrally to end in a sharp apex. It is seventeen microns long. The palpal tarsus originates from the ventral surface of the tibia and opposes the terminal claw in thumb-like fashion. On the medial surface of the tarsus are three plumose setae. Laterally there are six plumose setae and a single striated sensory seta at the base, and apically there are three striated sensory setae (Fig. 9).

The maxillae extend to the tip of the chelicerae and are completely fused along the mid-line. At the tip they are divided into three lobes. The median ventral lobe is without setae but bears a lateral pair of horn-like projections. There are three nude setae on each of the lateral lobes, which probably represent the larval galeae and the galeal setae. Posteriorly and laterally there are seven plumose setae on each maxilla.

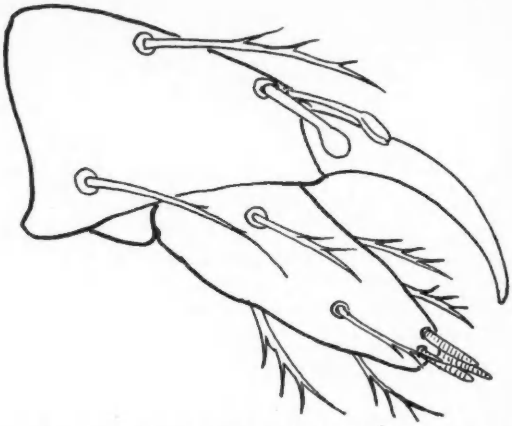

FIG. 9. Medial view of terminal palpal segments of the nymph of *A. indica.*

The chelicerae cover the maxillae dorsally. Each chelicera consists of a long narrow basal segment and a distal, falcate, chitinous segment that bears a row of from ten to fifteen teeth on its dorsal edge. The stigmata open on the median face of the basal cheliceral segments near their proximal ends. The tracheal trunks extend posteriorly and are similar to those of the larva. The mouth is situated between the chelicerae just dorsal to the maxillae.

Dorsally the gnathosoma is covered by the anterior portion of the idiosoma. Just above the middle of the basal cheliceral segment there is an epistome that bears a single plumose seta. This seta is homologous to the anterior-median scutal seta of the larva. The anterior margin of the epistome is ornamented with numerous fine teeth (Fig. 10).

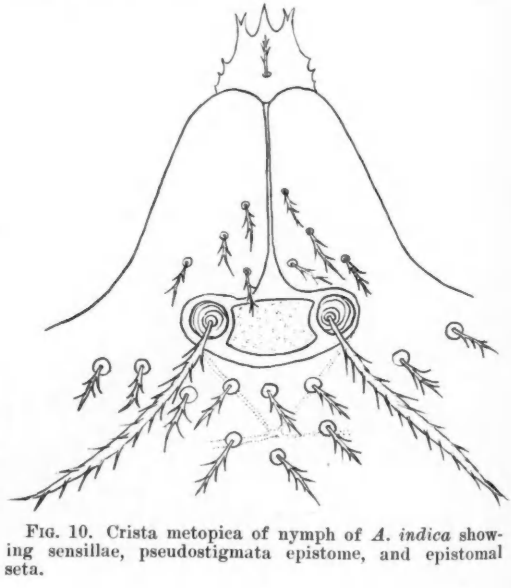

FIG. 10. Crista metopica of nymph of *A. indica* showing sensillae, pseudostigmata epistome, and epistomal seta.

The legs are arranged in two groups; the coxae of legs I and II are contiguous and flank the gantho-soma, Legs III and IV have fused coxae just posterior to the constriction that divides the idiosoma into propodosoma and hysterosoma. There are about fifteen plumose setae on coxa I. Trochanter I has two plumose setae, basifemur about ten plumose setae, telofemur about fourteen, tibia over twenty plumose setae and four striated sensory setae, and the tarsus has numerous plumose setae and at least fourteen striated sensory setae. There are a pair of terminal tarsal claws on each leg. Tarsus I is 69 microns long and 39 microns wide. Tibia I is 58 microns long (Fig. 11). Leg II is considerably shorter and narrower than leg I but has the same number of segments and similar but fewer setae on each segment. Leg III is about the same size as leg II but the setae are similar to leg IV. Coxa IV has thirteen plumose setae, six plumose setae are on the trochanter, five plumose setae on the basifemur, six plumose setae are on the telofemur, the genu has seven plumose setae and five striated sensory setae, there are seventeen plumose and five striated sensory setae on the tibia, and on the tarsus there are about twenty plumose setae and only two striated sensory setae.

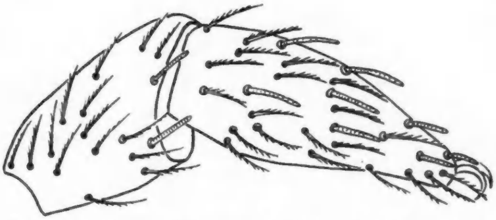

FIG. 11. Terminal segments of leg I of nymph of *A. indica*.

The idiosoma is divided into two sections by a deep cleft between the anterior propodosoma and the posterior hysterosoma. This division is responsible for the figure-eight shape that is so characteristic of many trombiculid nymphs and adults. The anterior portion of the propodosoma has only a few dorsal plumose setae flanking the median crista metopica, and from four to six on the ventral side between the anterior pairs of coxae. Behind the sensillary area of the crista metopica the propodosoma is expanded into a pair of shoulders that are thickly clothed with plumose setae both dorsally and ventrally.

The dorsal plate or scutum of the larva is represented in the nymph by the crista metopica (Fig. 10). The pseudostigmata are in an expanded posterior section of the crista metopica known as the sensillary area. The pit-like pseudostigmata are separated from the rectangular body of the sensillary area by a sclerotized bar. The cuticle of the rectangular area is ornamented by fine pits such as are found on the larval scutum. Except for the posterior expanded portion, the crista metopica consists of a sclerotized groove that reaches the anterior margin of the idiosoma. The thin, expanded epistome extends from the anterior end of the crista metopica. Posterior to the sensillary area the crista metopica is submerged beneath the cuticle and consists of two sclerotized bars that extend from the pseudostigmata to meet in the mid-line about fifteen microns posterior to the sensillary area and then fuse to form a narrow transverse band that is about forty microns long. The pseudostigmatic organs are long, 68 microns, plumose, and spatulate.

The hysterosoma is thickly clothed with plumose setae both dorsally and ventrally. All of the setae are of the same type. Ventrally on the hysterosoma are the fused coxae of legs III and IV, the genital opening, and the uropore or anal opening.

The genital opening (Fig. 12) is in the midline just posterior to coxae IV. Externally it is closed by a pair of genital plates that are about 45 microns long by 20 microns wide. Their median margins are straight while their other margins are an even curve so that together they give the genital region an elliptical shape. Each genital plate bears three nude setae. Beneath the genital plates, apparently on the dorsal wall of the genital atrium are two pairs of genital suckers. Both pairs of suckers are elliptical in outline. The anterior pair are larger, 14 microns, than the posterior pair, 10 microns long. All nymphs studied appear to have identical genital openings. It was not possible to differentiate males from females in the nymphal stage.

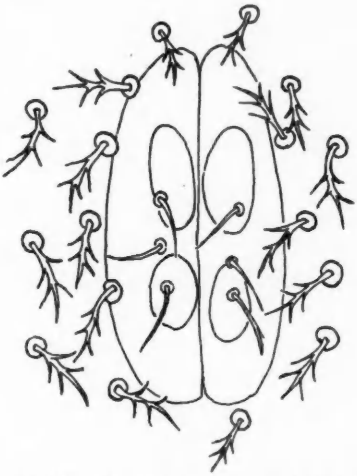

FIG. 12. Nymphal genital region of *A. indica*.

The anal opening is 35 microns posterior to the genital opening. It consists of a pair of anal plates similar to the genital plates but much shorter, 35 microns in length. The anterior halves of the anal plates are more heavily sclerotized than the posterior halves. Each anal plate bears about four plumose setae that are similar to those of the hysterosoma (Fig. 13).

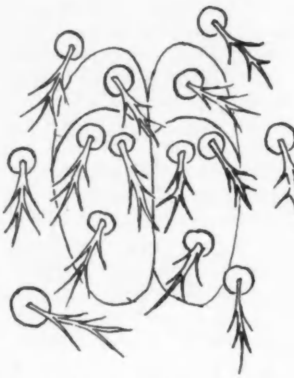

Fig. 13. Anal plates of nymph of *A. indica*.

Imagochrysalis—The imagochrysalis is similar to the nymphochrysalis. It develops inside of the nymphal skin as the nymphochrysalis develops inside of the larval skin. The horn-like projection found posterior to the larval scutum in the nymphochrysalis is present just posterior to the nymphal crista metopica in the imagochrysalis. The imagochrysalis is considerably larger than the nymphochrysalis measuring 750 microns in length.

Adult (Figs. 14-16)—Adults and nymphs are similar. Adults differ from nymphs in that they are larger, have more numerous setae, and have mature reproductive systems. The detailed description of the nymph will apply to the adult if these three differences are remembered. Therefore a complete description of the adult will not be given. Instead only a description of the palpi, which are identical in both sexes and the male and female genital openings will be considered.

The palpal coxae are imbedded in the body of the gnathosoma. Right and left coxae are united by a transverse sclerotized band as they are in the larva. The trochanter articulates with the coxa, is short, and bears no setae. There are five plumose setae on the expanded femur, nine plumose setae on the genu, and six plumose setae on the tibia. The tibia in addition bears the long, 22 microns, simple, curved, terminal claw; three claw-like setae with expanded tips clustered at the base of the claw; and four nude setae on its dorsal lateral surface. The palpal tarsus opposes the tibial claw in thumb-like fashion and bears about fifteen plumose setae, three apical striated sensory setae, and a single striated sensory seta on the lateral surface near the base (Fig. 14).

The female genital opening (Fig. 15) is closed by a pair of genital plates that are similar to those of the nymphs. On the posterior half of each plate there are four nude or slightly branched setae that correspond in position to the three nude setae seen in the nymph. Laterally and anteriorly the plates bear several of the setae that cover the entire idiosoma. Within the genital atrium, apparently on its dorsal wall, are three pairs of oval genital suckers. These are fourteen, fifteen, and twelve microns in length respectively.

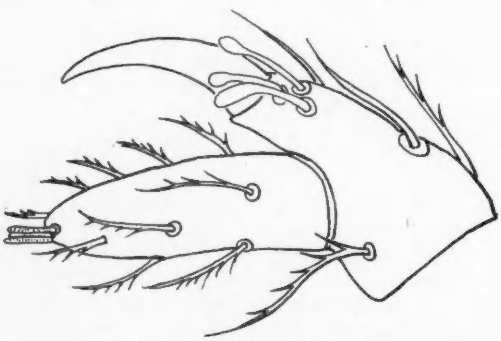

Fig. 14. Medial view of terminal palpal segments of adult of *A. indica*.

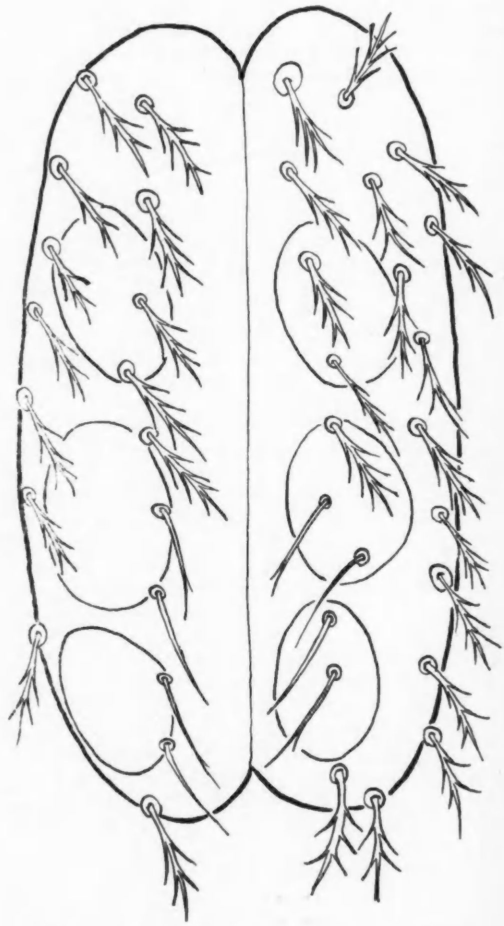

Fig. 15. Female genital opening of *A. indica*.

The male genital plates (Fig. 16) are broader than those of the female. They are provided with numerous plumose setae similar to those on the general body surface. In addition to the plumose body setae each plate bears a long specialized brush-like seta with long barbs, and four setae that are nude or have only one or two fine barbs similar to those on the genital plates of the nymphs. Within the genital atrium is a spade-shaped penis that is 40 microns long by 27 microns wide. A thinly sclerotized sac that is probably the seminal vesical connects with its posterior end. Lateral to the penis on the dorsolateral wall of the atrium are three pairs of genital suckers. The relative sizes of these suckers differ from those of the female in that the anterior pair are the largest. The length of the suckers is sixteen, fourteen, and twelve microns respectively.

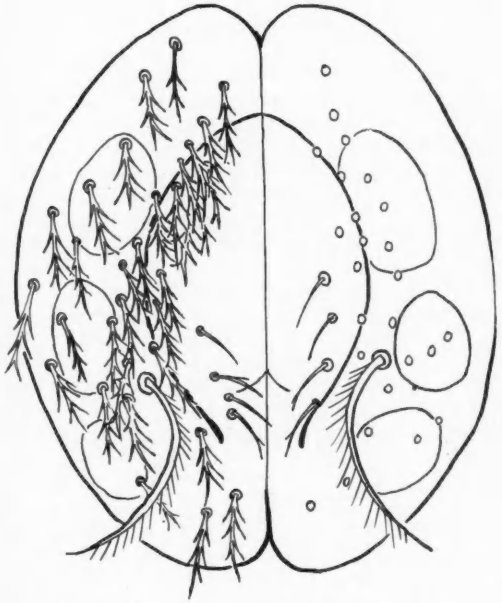

FIG. 16. Male genital opening of *A. indica.*

Discussion—The external morphology of trombiculid mites is used to the exclusion of other characteristics in establishing their systematic position. Most trombiculids are known only in the larval stage, and many of these are described only superficially. Nymphs and adults are even more imperfectly known. However certain morphological features of the group seem to be of a constant nature and can be discussed in general terms.

In the larvae the setae of the first four segments of the palps are constant in number and arrangement; one on the first or coxa-trochanter, one on the second or femur, one on the third or genu, and three, one dorsal, one lateral, and one ventral on the tibia. The setae may be of different types, but they are always present. The setae on the palpal tarsus are not constant in number or position with the exception of the striated sensory seta at its base. This seta is present in that position on all trombiculids that have been investigated. The chelicerae always consist of two segments, and the endoskeleton of the gnathosoma, described here, is to be found in all trombiculids. The legs vary considerably within the family. They may have six or seven segments, and the setae, although constant within a species, vary widely from one species to another. An urstigmen is always found associated with coxa I. While the scutum, its setae, and sensillae are variable within the family, they are always present although at times vestigial. The body setae are fairly constant in number within a species but differ widely in different species.

The deutovum, nymphochrysalis, and imagochrysalis of those species in which they are known, all have the characteristic horn-like projection posterior to the scutum or sensillary area.

The nymphs of all species of trombiculids that have been studied can be recognized by the fact that they have only two pairs of genital suckers. The nymphs of many species have two spine-like setae on each palpal tibia, but some may have more.

The adults of trombiculids can be recognized by the presence of three pairs of genital suckers. A penis can be seen in the male so that the sexes are readily differentiated. Whether other species have the specialized setae on the genital plates of the male that are described above is as yet undetermined.

Both nymphs and adults are characterized by their: hairy figure-eight shaped body, crista metopica and sensillae, epistome, hairy legs with expanded tarsi on leg I, and the relative positions of the legs. Eyes are variable and may or may not be present.

OBSERVATIONS IN THE LABORATORY

MATERIALS AND METHODS

Laboratory—A small room in an air-conditioned laboratory building was used to conduct studies on living trombiculids. In previous work with maintaining living trombiculids in small glass containers, it was found that rapid changes in temperature invariably caused such changes in the distribution of moisture that it was difficult to maintain trombiculids in a healthy condition for extended periods. While the air-conditioned atmosphere of the laboratory did not completely correct this condition, it greatly alleviated it, and facilitated the work. The controlled temperature and humidity also made it possible to maintain infected animals in the laboratory in small cages without providing them with nesting materials.

Hosts—A more or less continuous program of live trapping was conducted by the laboratory of mammalogy under the direction of Lt. Commander D. H. Johnson in order to maintain a constant supply of infested rats from which engorged chiggers could be obtained. Live rats brought into the laboratory in traps were placed singly in a rubberized cloth bag.

The rat was grasped behind the neck while it was in the bag. Leather gloves were worn to protect the hands because some of the larger rats were capable of biting through the bag. The bag was then turned inside out so as to expose the head and ears of the rat. Visual examination of the ears was made to determine whether or not large colonies of chiggers were present. If no chiggers were present the rat was sacrificed and discarded unless uninfested animals were desired. If chiggers were present the rat was placed in an empty cage constructed especially for the collection of ectoparasites.

The cages were made of galvanized sheet metal. They were rectangular and measured twelve inches long by eight inches wide by six inches high and were supported on each corner by legs made of straight metal rods that projected one inch from the floor of the cage. The covers of the cages, also of galvanized sheet metal were made so that they slid into place in such a way that an ectoparasite would have to pass three baffles in order to escape through the cover. The floor of the cages was made of quarter-inch mesh hardware cloth so that any ectoparasite dropping from the rats would eventually fall through the floor of the cage. When in use cages were placed on shallow enameled trays that were slightly larger than the cages. These in turn were placed in large 36 inches by 24 by 8 inches photographic trays that were kept coated with a thin layer of dimethyl phthalate in order to kill any mites that left the smaller trays on which the cages rested. Four cages with their black enameled trays were accommodated conveniently in each of the large trays.

When animals were kept in the cages, the cages and trays were cleaned every day and sterilized by scrubbing them with a solution of lysol. Animals were fed on moistened Purina animal food and remained healthy even though no water was available for drinking. Food was given at night and the cages and trays cleaned in the morning. In this way the trays under the cages remained fairly clean during the day so that detection of ectoparasites on them was not made difficult by excessive collections of urine and fecal pellets.

In order to immobilize rats for examination of their ears under the dissecting microscope, a cone was made of quarter inch mesh hardware cloth that would just accommodate a rat, when the cone was placed over an opening in the cage that contained a rat, the rat could readily be teased into entering the cone. Once in the cone the rat forced its way as far as it could toward the apex. The cone was then removed from the opening in the cage and its base closed by means of a roll of cheese cloth prepared for that purpose. The cheese cloth was held in place by metal rods pushed through the mesh in the hardware cloth. It was found that no injury resulted to the rats by this procedure and that the ears of the rat could be pulled through the mesh for careful examination. Rats were never kept in cones for more than two hours, even though they appeared to be quite content in them and for the most part remained motionless. When it was desired to return the rat to its cage, the rods and cloth plugs were removed and the open base of the cone quickly applied to a suitable opening in the empty cage. The rat then backed out of the cone into the cage.

Culture dishes—The most satisfactory containers for maintaining the free-living stages of *A. indica* in a healthy condition were low-form glass weighing bottles 50 millimeters in diameter and 30 millimeters high provided with ground glass stoppers. These bottles could be hermetically sealed by coating the stoppers with stopcock grease. It was found to be desirable to use tightly sealed dishes in order to prevent excessive loss of moisture. Dishes were prepared for the reception of mites in several ways. The object of adding material to the dishes was twofold, one to provide a substratum that would hold enough absorbed water to maintain a high relative humidity in the dish without exposing the mites to droplets of moisture and two to provide isolated retreats where quiescent stages might develop. Sterilized soil and porous pieces of coral were used at first. Later it was found that plaster of Paris made a suitable reservoir for absorbed water. The most satisfactory culture preparations were made by mixing ten grams of powdered plaster of Paris with one to one half of a gram of activated charcoal in a culture dish. After the powder is thoroughly mixed five and a half cubic centimeters of water are added and mixed with the powder. As the plaster sets it is spread evenly over the bottom and sides of the dish and its surface is smoothed or roughened as desired. Embryological watch glasses, glass cells of two cubic centimeter capacity, test tubes, Stender dishes, and hollow-ground glass slides were also used to maintain the free-living stages of *A. indica*. Of these, only the embryological watch glasses prepared with activated charcoal and plaster of Paris compared favorably with the weighing bottles. The watch glasses were sealed with plate glass covers by means of stopcock grease.

Trombiculids—Engorged chiggers were obtained from several sources and placed in prepared culture dishes of various types. At first chiggers from the trays under the caged rats were used, but it soon was discovered that a simpler way of obtaining engorged chiggers in large numbers was to remove them from the ears of rats that had been kept in cages for from five to ten days. Some engorged chiggers from freshly trapped rats were also used. Free-living nymphs and adults, collected with the aid of modified Berlese funnels, were used in some cultures. After mites had been added to the cultures they were placed in an incubator that was maintained at a constant temperature of thirty-two degrees centigrade. Cultures were examined at room temperature which was maintained at about twenty-five degrees centigrade with a relative humidity of about seventy. The relative humidity inside of the culture dishes was kept at saturation by the addition of a few drops of dis-

tilled water when the substratum became too dry to produce droplets of condensed moisture on the inside of the ground glass covers.

Foods—Many materials were added to the culture dishes as food for the free-living stages. Pieces of potato, apple, fruit of *Ochrosia mariannensis,* rotten wood, puff ball,* papaya, sugar, butter, chicken's guano, noddy's guano, rat's feces, and millipede's feces were added to the cultures containing nymphs and adults. Guano, potato broth, serum, and a nutrient solution of fats, carbohydrates, amino acids and vitamins, were blended with the plaster and charcoal coating on the sides of the dishes. Live millipedes, collembolans, cheese-mites, and nematodes were provided for some cultures. Both cheese-mites and nematodes were cultured on nutrient agar in petri dishes so that a large supply was readily available. Numerous animals that occurred in the soil were concentrated and presented to nymphs and adults. Concentrates of soil were prepared by washing the animals out of the soil through a double thickness of cheese cloth. The soil to be concentrated was wrapped in a double thickness of cheese cloth. The cloth with enclosed soil was then dipped repeatedly into a beaker of water that was warmed to forty degrees centigrade. The water was then filtered and the animals and fine particles from the soil were added to the plaster. The animals ranged from protozoa through nematodes to small arthropods such as mites and collembolans. Unsterilized humus was also used both alone and with live millipedes. The presence of the millipedes inhibited the growth of mold on the decaying humus. The eggs of small arthropods were also used. Eggs of four species of mosquitoes were made available by the laboratory of entomology. *Drosophila melanogaster* and *Tribolium castaneum* were cultured in the laboratory so that eggs of these species would be available for feeding free-living stages. The fruit flies were fed on baker's yeast and banana. Gravid females were induced to lay eggs on banana skins, the eggs were then removed and placed in the cultures or stored in the refrigerator until needed. Eggs were dissected from gravid female beetles and placed at once in the cultures. Eggs of mosquitoes and flies frequently hatched in the culture dishes so that first instar larvae were available for the mites as food. The eggs and first instar larvae of ants, *Anoplolepis longipes* were collected and used for food for nymphs and adults.

BEHAVIOR OF CHIGGERS ON LABORATORY ANIMALS

Distribution—Chiggers or larvae of *A. indica* were found attached singly or in colonies only in the ears of *Rattus mindanensis.* Examinations of numerous hosts never yielded chiggers on other parts of the body. *A. indica* larvae were usually clustered in colonies deep in the concha near, or at times in, the external auditory meatus. They produced an encrusted lesion at their site of attachment, but did not cause a severe reaction such as some species do on men. Colonies of over one hundred specimens were not unusual in the ear, but the usual size of the colony was about thirty specimens. In some way the chiggers managed to attach in closely packed groups so that their bodies were contiguous and gave the appearance of tiles in a mosaic.

Feeding habits—*A. indica* larvae attach and feed in the same manner as other members of the family. They grasp the skin of their host with the palpal claws, elevate the posterior end of the body so that they are supported only by the palps and the first pair of legs, and pierce the skin of the host with the sharp terminal apical segments of their chelicerae. Soon thereafter they secrete a saliva that digests the tissue of the host. A reaction between the saliva and host tissue produces a straw-like feeding tube through which lymph and digested tissue may be sucked into the chigger. Chiggers are not known to feed on blood. The tube elongates on feeding and may become longer than the animal that is producing it. Examination of the lesion produced by the attachment of a colony of *A. indica* shows it to be riddled by the feeding tubes. Ewing 1944 discusses the feeding habits of other chiggers.

During engorgement larvae may increase in length from 176 microns to 394 microns. Enlargement is accomplished by expansion posteriorly and laterally. White spherical pellets of waste material were frequently seen to be associated with fully engorged specimens.

Detachment—Both engorged and unengorged specimens detach themselves on the death of the host although in most cases some of the members of a colony do not succeed in freeing themselves from the host but die in place. Chiggers also drop from living animals. However the majority do not detach singly but seem to come off in groups. Examination of the trays under the cages of infested *Rattus mindanensis* demonstrated this fact. Detached chiggers were recovered from a rat caged 15 May 1945 as follows: one the first day, two the second day, six the ninth day, while some were still present when the rat was sacrificed on the fifteenth day. A rat caged 3 June 1945 produced two chiggers the third day, thirty chiggers the sixth day, two chiggers the ninth day, four chiggers the tenth day, one chigger the eleventh day, four chiggers the twelfth day, and several chiggers were found still attached on the thirty-second day when the animal was sacrificed. Another rat also caged 3 June 1945 produced one chigger the third day, one the fifteenth day, and none when it was killed on the thirty-second day. A rat caged on 9 June 1945 produced two chiggers the second day, twenty-one chiggers the third day, five chiggers the fourth day, and none when it was killed on the thirty-third day. The above data can be summarized by pointing out that four chiggers were recovered singly, six were recovered in pairs, nineteen were recovered in groups of from four to six, and fifty-one were recovered in two groups of more than twenty each.

The longest time that chiggers of *A. indica* were known to remain on a host was thirty-two days. That the chiggers were on the host during that time is certain since the host was placed in a clean cage every day during the period of its captivity. Chiggers kept on the host in the laboratory for a minimum of five days had taken sufficient nutriment to be used routinely as a source of engorged chiggers for culture experiments. The actual length of time that these chiggers were on the host was not determined.

Attachment—Several attempts were made to induce larvae of *A. indica* to attach to laboratory animals so that chiggers might be fed under controlled conditions. On 9 June chiggers that were not completely engorged were removed from the ear of a dead *Rattus mindanensis*. They were then entangled in cotton which was placed on a strip of adhesive tape. The tape was attached to the ear of a laboratory mouse. The following day the chiggers could not be found and were not on the mouse. On 4 August 1945 twenty-seven unfed chiggers obtained from Berlese funnels were placed in the ear of a white mouse. After one day none could be found attached to it. Portions of the root system of an epiphytic fern that contained numerous chiggers were placed in the cages of six white mice. None of the mice became infested. Attempts to infest a giunea pig and chicken by placing unattached chiggers on them were likewise unproductive. On 30 August 1945 four unfed chiggers collected with the aid of a Berlese funnel were placed on the ears of a small *Rattus mindanensis*. The rat was examined with a dissecting microscope while the chiggers were placed in its ear. The chiggers, as soon as they were placed on the ear, orientated themselves and moved rapidly toward the external auditory meatus. The following day four chiggers were found in the external auditory meatus. All were attached but had not yet increased in size. They were removed and placed on the ear of a second rat. They did not orient themselves on the ear of the second rat but moved about in circles. Examination of this rat on the second day revealed that the chiggers had not attached. On 14 September 1945 eighteen chiggers were placed on the ear of a rat. On 24 September the rat was sacrificed. Five engorged chiggers were removed and these were reared to the nymphal stage. On 18 September thirty chiggers were placed in the ear of a rat. Ten days later the rat was sacrificed and yielded a single engorged chigger. This chigger was reared to the adult.

Cultures

Introduction—Many attempts were made to maintain the free-living stages of *A. indica* in the laboratory. These efforts will be presented by first summarizing the results obtained in general, next giving records of representative and significant cultures, and finally describing certain observations made on cultures during routine examinations.

General results—Seventeen cultures were made with engorged chiggers that were collected from trays under cages that housed infested rats. One of the cultures consisted of a single chigger in a glass cell of two cubic centimeters capacity whose bottom and sides had been coated with blackened plaster of Paris. Although the cell was closed by a glass cover and sealed with stopcock grease the chigger became desiccated before any development occurred. Two cultures were made by adding chiggers to autoclaved soil in weighing bottles. The chiggers became lost in the soil but examination of one of the cultures fifteen days after the chiggers were added revealed a single dead nymph. Seven weighing bottles that had a thin coating of plaster of Paris on their bottoms were used as culture dishes. No nymphs developed from the chiggers placed in them. The chiggers became desiccated and covered with mold. Twenty-one chiggers were put in a weighing bottle whose sides and bottom were coated with roughened plaster of Paris. Seventeen days later a single nymph was seen. No further development was noted. Six cultures were made by adding chiggers to weighing bottles that were coated on sides and bottom with blackened plaster of Paris. Five of these cultures had roughened plaster of Paris and in three of them nymphs developed. These nymphs were offered millipede feces for food but no further development occurred. No nymphs developed in the single culture with smooth plaster.

Fifty-five cultures were started with engorged chiggers removed from the ears of dead rats. A supply of engorged chiggers was insured by caging the animals for from five to ten days before killing them. One culture was made by adding chiggers to a ground-glass slide in which there was moist sterile sand. It became desiccated without developing. Three cultures were made using plaster coated embryological watch glasses. A single nymph developed. Five per cent sodium proprionate was added to the plaster in another embryological watch glass in order to inhibit the growth of fungi. No fungi developed but the surface of the treated plaster was unsatisfactory for the chiggers. They were immobilized and did not develop, but died. Chiggers were placed in a weighing bottle with pieces of moist sterile coral. No development occurred. Chiggers were added to five weighing bottles that contained moist sterile soil. After twenty days all cultures had a vigorous growth of fungi. One dead nymph was found. One culture was made with a weighing bottle whose bottom had a thin coat of plaster of Paris. No development occurred. A test tube coated with blackened plaster was used for one culture. Nymphs developed in this tube but after thirty-one days all were dead. Weighing bottles coated inside with roughened, blackened plaster were used for eight cultures. Nymphs appeared in all of them in five days, except one in which the nymphs appeared in four days. Some of the nymphs were used in establishing sub-cultures. One of these became an adult eight

days after it had been put in the sub-culture. Concentrations of soil dwelling animals were given to it for food. Cultures were kept up to forty-five days. Millepede feces were used as food for one of the cultures, millipede feces and soil concentrate were used for another, and the remainder were given soil concentrates. One culture was made in a Stender dish coated with blackened plaster. After nymphs developed a sugar solution was added to the plaster. A mite *Tyrophagus lintneri* contaminated this culture and lived well. No development of the nymphs occurred. Two wide-mouthed bottles coated on the inside with chicken's guano and soil were used. Nymphs developed in one of them. Fungi grew rapidly in both cultures and the nymphs did not develop into adults. Weighing bottles that were lined with blackened plaster of Paris were used for twenty-four cultures. In all but one, nymphs appeared in from four to six days. Adults developed in five of the cultures and one sub-culture made from a sixth culture. Of the cultures in which adults developed one was fed on humus to which a live millipede had been added, two were fed on eggs of *Drosophila melanogaster,* and two were fed on eggs of *Culex jepsoni* and *Culex quinquefasciatus.* Humus with a live millipede was used as food in five cultures that produced no adults. Soil concentrates, potato broth, and a nutritive solution were offered as food for other cultures, but no adults appeared. No food was added to five cultures, and the nymphs did not develop into adults. Plaster blackened with ten per cent instead of five per cent activated charcoal was used to coat seven weighing bottles. Nymphs appeared in all cultures in from five to six days. Adults developed from the nymphs in all cultures in from nine to fourteen days. In one culture eggs were seen eleven days after the adults were first seen, and thirty chiggers were produced. All of these cultures were fed on eggs of small insects. Eggs of *Tribolium castaneum* were used in one culture. Eggs of *Aedes aegypti* and *Aedes pandani* were used for food in a second culture. Eggs of *Culex jepsoni* and *Culex quinquefasciatus* were used for three cultures, and eggs of *Drosophila melanogaster* were used for one culture. Many sub-cultures were made from the primary cultures in which nymphs developed. Sub-cultures were used primarily to test the suitability of various materials as food for the nymphs. One sub-culture was made in a Stender dish coated with blackened plaster. Nematodes were provided as food but no adults developed. Four embryological watch glasses that contained soil and chicken guano were used but no development occurred. Six glass cells coated with blackened plaster served for six sub-cultures. No food was added to two, fungus was added to two, and millipede feces were used in the remaining two sub-cultures. No adults developed. Nineteen sub-cultures were made in weighing bottles coated with black plaster. The following foods were added to the cultures that failed to produce adults: millipede feces in one, decaying wood in one, dried human serum in three, root of papaya in one, puff ball in one, collembolans in two, nematodes in two, potatoes in one, potato broth in one, *Tyrophagus lintneri* in one, butter in one, and one with humus and live millipedes. The three sub-cultures in which adults developed were fed on soil concentrate, eggs of the ant *Anoplolepis longipes* and unidentified eggs, and the eggs of *Drosophila melanogaster* respectively. Forty-two sub-cultures were made with embryological watch glasses coated with blackened plaster. No adults developed in these when provided with the following foods: one with potato broth, seven with potato broth and guano of the noddy tern *Anous stolidus,* six with a nutritive solution of pure chemicals, four with millipede feces, two with pieces of papaya, two with rat feces, two with fruit of *Ochrosia mariannensis,* two with potato roots, two with *Tyrophagus lintneri,* two with the stem of an epiphytic fern, two with fern soaked in nutritive solution, four with humus and live millipedes, four with chicken guano, one with *Anoplolepis longipes* eggs and one with Culex eggs.

In addition to cultures started with engorged chiggers, nymphs and adults collected with the aid of Berlese funnels were also used. These cultures were made in order to study the behavior of nymphs and adults, and to attempt to develop a satisfactory method of obtaining chiggers from adults. Eleven cultures were made with weighing bottles that were coated with blackened plaster. They were kept from twenty-nine to forty-eight days. In one of these cultures an unattached chigger was found after forty days. This culture had been fed on eggs of *Culex jepsoni* and *Culex quinquefasciatus.* Eggs were observed in two other cultures within a week after the introduction of adults. Fifteen individual adults were added to embryological watch glasses that were lined with blackened plaster. Eggs were seen in five of these cultures. On the second day three contained two eggs and one contained a single egg while the fifth culture had two eggs on the third day.

Records of cultures—Cultures whose records are given were chosen because they were representative of several cultures or because interesting observations were made on them.

Mite Culture No. 4

14 May 1945—Sterile soil was placed in a sterile weighing bottle so that it was half full. The soil was then saturated with distilled water. An ear of a rat that was infested with chiggers was placed in the jar at 1025. The rat, a female of *Rattus mindanensis* had been captured in a live trap on Oca Point.

16 May 1945—Removed ear from jar at 0905. A number of chiggers still walking about on ear. These removed and placed on soil. Some chiggers mounted and identified as *A. indica.*

18 May 1945—Much moisture condensed on inside of bottle. Mold growing on surface of soil. Cover removed for twenty-five minutes in order to dry culture.

20 May 1945—Cover removed to evaporate moisture.

22 May 1945—Cover removed to evaporate moisture.

24 May 1945—Much condensed moisture in bottle. Cover removed to evaporate moisture.

2 June 1945—Culture placed in incubator at 32° centigrade.

3 June 1945—Condensation in bottle, opened to dry.

5 June 1945—Bottle carefully examined. One dead nymph found entangled in a luxurious growth of fungal hyphae.

Mite culture No. 4 is typical of those that were made with soil.

The soil held moisture poorly and always developed a luxurious growth of fungus which frequently attacked the developing mites.

Mite Culture No. 30

13 June 1945—*Rattus mindanensis* caged on 6 June found dead in cage. Approximately one hundred chiggers found in ears of rat removed and placed in a weighing bottle prepared as follows: 10 grams of plaster of Paris were mixed with 0.5 grams of activated charcoal and 7 cc. of distilled water and spread over the bottom and sides of the bottle.

17 June 1945—Many larvae have a "double-decker" appearance. At 1415 removed material from culture on which fungi were growing. Culture examined every hour until 2120 without seeing any nymphs. 2240, 2 nymphs seen. 2320, 3 nymphs seen. 2355, 4 nymphs seen. 18 June 1945—0030, 5 nymphs seen. 0105, 7 nymphs seen. 0125, 10 nymphs seen. 0300, 12 nymphs seen. 0325, 13 nymphs seen. 0335, 14 nymphs seen. 0800, many nymphs seen, removed larval skins and several nymphochrysalises for mounting.

Nymphs observed during emergence from nymphochrysalis. Larval skin splits transversely between the scutum and horn-like projection just posterior to the scutum. Anterior legs emerge first, followed progressively by other legs. Appendages are cleaned while emerging. The larval skin which has been stretched to contain the developing nymph now shrinks, and the body of the nymph emerges from it by sending wave after wave of contraction toward the posterior end of the body. The nymph is wet when it emerges and is brownish in color. It dries in about one minute and then appears to be salmon-white. The nymph cleans itself with its palps. The palpal thumb is active in this process. The entire process of emerging takes only five minutes when the larval skin is anchored in place, but takes up to ten minutes if the larval skin is unattached. The exoskeleton of the nymph is pliable and portions of the larval skin that adhere to the freshly emerged nymph are removed by the nymph squeezing its way through narrow crevices in the plaster. 0900 1 cc. of millipede feces added to culture as food for nymphs.

21 June 1945—Six nymphs removed to start sub-cultures.

23 June 1945—Nymphs on cover of bottle trapped in condensed moisture, returned to plaster. Fourteen nymphs removed to start sub-cultures.

24 June 1945—Seven nymphs removed to start sub-cultures.

25 June 1945—Fifteen nymphs removed to start sub-cultures.

26 June 1945—Nine nymphs removed to start sub-cultures. One sub-culture to which four nymphs had been added at 0930 was examined at 1030. One nymph had a drop of fluid on the third leg near the body and moved sluggishly as though it were injured. A rapidly moving nymph approached it and attached its front legs to the opisthosoma of the apparently injured nymph. The attacker then brought its ganthosoma as close to the posterior end of its victim as the plumose setae on the victim would permit. The attacker remained anchored in place while the other mite moved away. The opisthosoma of the retreating nymph stretched to twice its normal length before the hold was broken. The injured mite made good its escape, and the attacker made no further efforts to follow it.

27 June 1945—Three nymphs removed to start sub-cultures.

9 July 1945—Removed millipede feces, added soil concentrate.

10 July 1945—Added additional soil concentrate. One nymph found in soil concentrate that had been added 9 July. Nymph returned to plaster.

13 July 1945—Added fresh soil concentrate. One nymph returned to plaster from old food.

15 July 1945—Added fresh food. One nymph in old food returned to plaster.

25 July 1945—Mounted dead nymph, culture discarded.

Mite culture No. 30 was typical of many cultures, made in weighing bottles coated with blackened plaster. It was chosen for description since interesting observations were made on the habits of the nymphs.

Mite Culture No. 89

16 August 1945—Twenty-seven chiggers from two *Rattus mindanensis* that had been caged for eight days were placed in a weighing bottle coated with blackened plaster.

21 August 1945—Twelve nymphs seen.

23 August 1945—One nymph added to each of twelve embyological watch glasses that were lined with blackened plaster. Covers sealed with stopcock grease. Food placed in watch glasses as follows: 200—1.5 cc. of nutrient solution, 201—1.4 cc. of nutrient solution, 202 and 203—ripe papaya, 204 and 205—rat's feces, 206 and 207—pulp of the fruit of *Ochrosia mariannensis,* 208 and 209—blackened plaster soaked in nutrient solution.

24 August 1945—Sub-cultures examined 0900. 200—nymph dead; 201—nymph on cover, moves slowly; 202—nymph in good condition in hole in plaster under piece of papaya; 203—nymph in good condition, posterior end dark; 204—nymph in fair condition; 205—nymph not found; 206—nymph in

poor condition anterior legs elevated, mold and maggot on pulp of *Ochrosia mariannensis* removed from culture; 207—nymph in fair condition, posterior end wrinkled, food moldy; 208—nymph in excellent condition; 209—nymph not found; 210—nymph in excellent condition; 211—nymph in excellent condition. Made four additional sub-cultures with food as follows: 212 and 213—potato root from young plant, 214 and 215—more than one hundred *Tyrophagus lintneri* in each.

25 August 1945—Examined sub-cultures. 200 and 201—with a heavy growth of fungi, discarded; 202—nymph in excellent condition, mold on papaya; 203—nymph in excellent condition, mold on papaya; 204—left forelimb of nymph damaged, mold; 205—nymph not seen; 206—nymph in excellent condition; 207—nymph on cover with swollen anterior end and reduced posterior end, mold; 208—nymph not seen; 209—nymph not seen; 210—nymph pale in good condition, mold; 213—nymph in good condition, mold; 214 and 215—nymphs not found.

26 August 1945—Sub-cultures examined. 202—nymph on cover in poor condition; 203, 204, and 205—nymphs not found; 206—nymph on cover, left foreleg injured; 207—nymph in good condition; 208 and 209—nymphs not seen; 210—nymph pale in good condition; 211 and 212—nymphs not seen; 213—nymph on cover; 214 and 215—nymphs not seen.

27 August 1945—Sub-cultures examined. 202—nymph in good condition; 203—nymph not seen; 204—nymph on cover, left foreleg impaired; 205—nymph not seen; 206—nymph motionless in cavity; 207, 208, and 209—nymphs not seen; 210—nymph in good condition; 211—nymph not seen; 212—nymph on cover, in poor condition; 213—nymph in good condition; 214—nymph active, posterior end reduced in size; 215—nymph in good condition.

28 August 1945—Examined all sub-cultures. 202—nymph in good condition, much mold in dish; 203—nymph not seen, mold on papaya; 204—nymph on plaster, left foreleg crippled, posterior end wrinkled, appears to be feeding on plaster; 205—nymph not seen; 206—nymph on cover, returned to plaster, moves slowly; 207—nymph dead, dead maggot also found; 208 and 209—nymph not seen; 210—nymph in excellent condition; 211—nymph not seen; 212—nymph pale, moves awkwardly; 213—nymph quiescent; 214—nymph in good condition; 215—nymph not seen.

29 August 1945—Examined all sub-cultures. 202—nymph in good condition, moves slowly; 203—nymph not seen; 204—nymph in good condition except for injured leg; 205—nymph not seen; 206—nymph motionless; 208 and 209—nymph not seen; 210—nymph trapped under cover, mounted; 211—nymph not seen; 212—nymph pale, moves feebly; 213—nymph on cover in good condition; 214—nymph pale, and quiescent; 215—nymph pale, forelegs elevated.

30 August 1945—All sub-cultures examined. 202—nymph trapped in water on cover; 203—nymph not seen; 204—nymph trapped in water on cover; 205—nymph not seen; 206—nymph pale, forelegs elevated; 208, 209, and 211—nymphs not seen; 212—nymph pale and quiescent; 213—nymph pink and quiescent; 214—nymph quiescent, forelegs elevated. One nymph seen in main culture.

31 August 1945—All sub-cultures examined. 202—nymph not seen; 204—nymph moves slowly, foreleg apparently healed; 205—nymph not seen; 206—nymph pale, forelegs elevated, moves with poor coordination; 208, 209, and 211—nymphs not seen; 212—nymph pale and quiescent; 213—nymph on cover in grease; 214—nymph quiescent; 215—nymph quiescent.

1 September 1945—All sub-cultures examined. 202—nymph quiescent; 203—nymph not seen; 204—nymph caught in grease on cover; 205—nymph not seen, discarded; 206—nymph pale, forelegs elevated; 208, 209, and 211—nymphs not seen, discarded; 212—nymph quiescent, forelegs elevated; nymph in grease on cover; 214—nymph pale, moves feebly; 215—nymph quiescent, forelegs elevated.

2 September 1945—All sub-cultures examined. 202—nymph dead, mounted; 203 and 204—nymph not seen; 206, 212, and 213—nymph dead, mounted; 214—nymph pale, quiescent; 215 nymph pale, quiescent.

4 September 1945—Examined sub-cultures. 214—nymph quiescent; 215—nymph dead, mounted; other sub-cultures discarded.

5 September 1945—Examined sub-culture. 214—nymph dead.

9 September 1945—Discarded main culture, examination revealed one dead nymph covered with mold.

The records on mite culture No. 89 are reproduced to demonstrate the manner in which sub-cultures were made and used. The use of embryological watch glasses allowed examination of the cultures without opening them unless manipulation of food or specimens was desired. As can be seen from the above records, when the nymphs approached death the forelegs were elevated and movement was greatly reduced. It is doubtful that any of the foods provided for the nymphs were eaten. Certainly none of them were satisfactory.

Mite Culture No. 115

1 October 1945—Over one hundred chiggers from ears of *Rattus mindanensis* that had been caged for ten days, put into a weighing bottle that was coated with blackened plaster.

6 October 1945—Saw seven nymphs, six eggs of *Drosophila melanogaster* placed in center of plaster.

7 October 1945—Removed old Drosophila eggs, added forty-nine new ones.

8 October 1945—Saw seven nymphs, added fifteen eggs, some of old eggs were collapsed.

9 October 1945—Saw five nymphs, all but two eggs collapsed, six eggs added.

10 October 1945—Saw two nymphs, all eggs collapsed, added six eggs.

11 October 1945—Saw four nymphs, four eggs collapsed, collapsed eggs removed, added twelve eggs.

12 October 1945—Saw seven nymphs, ten eggs collapsed, removed, added nineteen eggs.

13 October 1945—Saw three nymphs, all eggs collapsed, removed, added twenty-five eggs.

14 October 1945—Saw four nymphs, eighteen eggs collapsed, removed all eggs, added twenty-five eggs.

15 October 1945—Saw nine nymphs and one imagochrysalis. Thirteen eggs collapsed, removed all eggs, added twenty eggs.

16 October 1945—Saw six nymphs, six eggs collapsed, eggs removed, six eggs added.

17 October 1945—Saw one nymph, four eggs collapsed, removed all eggs, added twelve eggs.

18 October 1945—Saw two adults (adults can be recognized under the dissecting microscope by their greater size, more numerous body setae, and the presence of characteristic depressions in the hysterosoma caused by the attachment of the dorsal body musculature), seven eggs collapsed, removed all eggs, added twenty eggs.

19 October 1945—Eight collapsed eggs removed, added eight eggs.

20 October 1945—Saw two adults, seven eggs collapsed, removed all eggs, added forty-three eggs.

21 October 1945—Removed one collapsed egg.

22 October 1945—Nine eggs collapsed, removed all eggs, added forty-one more eggs.

23 October 1945—Twenty collapsed eggs removed, added twenty to replace them.

24 October 1945—Saw six imagochrysalises, eight collapsed eggs removed, added twenty-two eggs.

25 October 1945—Two imagochrysalises developed into adults, eight collapsed eggs removed and replaced with eight fresh eggs.

26 October 1945—Saw four adults and three imagochrysalises, removed sixteen collapsed eggs, added nine eggs, removed four adults for sub-cultures.

27 October 1945—Saw two adults and two imagochrysalises, removed nine collapsed eggs, added nine eggs.

28 October 1945—Saw one adult and two imagochrysalises, all eggs collapsed, added nine eggs and a few drops of distilled water.

29 October 1945—Saw one adult and two eggs of *A. indica* both appear to be in good condition.

31 October 1945—Saw five adults, all eggs collapsed, added twenty-three eggs.

1 November 1945—Saw eight adults, all eggs collapsed, added twenty more.

2 November 1945—Saw seven adults, eggs of *A. indica* first seen on 29 October overgrown with mold, all eggs collapsed, forty eggs added.

3 November 1945—Saw eight adults, all eggs collapsed, added sixty-one more.

4 November 1945—Saw eight adults, twenty-four eggs collapsed, removed, added twenty-four more.

5 November 1945—Saw sixteen adults, twenty-one eggs collapsed, removed all eggs, added forty-nine more.

9 November 1945—Saw fifteen adults and one larva. Larva placed on ear of uninfested *Rattus mindanensis*.

The record of mite culture No. 115 is given in detail because it is typical of cultures fed on the eggs of small insects. Mite culture No. 115 is also important since it was the first culture in which the complete life cycle of *A. indica* was encompassed. This culture was maintained by J. N. Strong until 16 December 1945. A total of thirty unattached chiggers were produced in this time.

Behavior of nymphs and adults—During routine examinations of the cultures, certain interesting observations were made on the behavior of the free-living stages. These will be discussed below.

Mite culture 101 was started on 19 September 1945 by adding thirty-six mites, nymphs and adults, to a weighing bottle that was coated with blackened plaster of Paris. On 20 September the following observations were made. At 1150 an adult was seen rolling an egg of *A. indica* about in front of itself by manipulating it with its palps. The palpal claws extended over the egg anteriorly while the palpal thumb engaged it posteriorly and pushed it along. In this manner the egg was rolled over and over and was even carried up the vertical walls of the bottle with no apparent difficulty. At 1200 several holes were made in the plaster with the point of a needle. Finally the egg rolled into one of the holes. The mite then scurried about over the top of the hole as if it were attempting to cover the egg. When unable to cover the egg the mite removed the egg from the hole. By 1220 the mite had placed the egg in a hole and removed it no less than nine times. The mite then moved away from the area where the holes had been pushed in the plaster. It rolled the egg as before. At 1225 it left the egg and approached a second adult. The two mites met each other face to face. They then proceeded to strike each other across the propodosoma with the expanded tarsi of the first pair of legs. This resulted in the depression of the propodosomas of both of the mites and an elevation of the opisthosoma at right angles to the propodosoma. When this occurred the genital and anal openings were no longer ventral but faced posteriorly. One of the pair then pivoted through 180° so that its genital opening faced the second mite. The genital plates of the mite that pivoted were protruded. The second mite failed to pivot. If it had the genital apertures of both individuals would have been contiguous. During the encounter described above a third adult found the abandoned egg and attempted to roll it away. It fumbled the egg just as the original owner returned and rolled it away. At 1230 almost as soon as it had regained its egg it met yet another adult. An encounter ensued similar to the one described above except that neither of them pivoted through 180°. At 1233 the original owner of the egg regained it. At 1235 it lost the egg and began rolling a piece of plaster that was approximately the same size as the egg. It recovered the egg in less than a minute and then dropped it to ward off another mite. Again it picked up the egg but at 1238 it abandoned it to approach a nearby mite. No contact was made before the egg was abandoned.

The mite rolling the egg seemed to be aware of the other mite when it was about a half millimeter away from it. The original mite returned to the egg only to leave it to explore a hole in the plaster at 1240. At 1242 it rolled the egg into the hole. The hole was abandoned at 1245, but the mite returned at 1248 after it had made a circuit of the culture bottle. At 1250 it again left the hole. At 1304 another mite entered the hole that contained the egg, but left when the first mite returned and attempted to remove the egg. At 1307 the first mite rested on top of the hole and remained quiet until 1311 when another mite tried to enter. This mite was repulsed by striking it with the front legs. At 1320 the mite on the hole was again disturbed by an intruder that was successfully driven away. At 1327 the mite left the hole but returned immediately. At 1340 the mite was finally evicted from the hole by a larger mite that entered the hole. The opisthosoma of the larger mite projected beyond the hole. Expansion and contraction of the opisthosoma occurred and it appeared as though the mite were feeding. It left the hole at 1345. Three mites explored the hole subsequently. At 1600 the hole was dissected and an empty egg shell was removed and mounted.

Mite culture 103 was made on 20 September 1945 by adding about fifty nymphs and adults, that were collected with the aid of a Berlese funnel, to a weighing bottle coated with blackened plaster of Paris. On 24 September 1945, eggs and first instar larvae of the ant *Anoplolepis longipes* were added to this culture. A large adult accidentally touched one of the ant larvae with its forelegs. It then went to the narrow end of the larva, grasped it and inserted its chelicerae. Once the chelicerae were inserted the opisthosoma of the adult began to expand and contract. Examination of the gnathosoma while this process was going on revealed that fluid was passing into the mite. An occasional bubble of air appeared in the stream of fluid so that the direction of flow was easily determined. Later four more mites, of which at least one was a nymph succeeded in taking nourishment from the same larva. Mites appeared to have swollen opisthosomas after they had fed. The ant larva on the other hand was reduced in size to such an extent that its cuticle was wrinkled. Ant eggs and first instar larvae were also added to mite culture 98 on 24 September 1945. This culture contained at least sixty nymphs that had come out of the nymphochrysalis on 18 September 1945. All appeared to be in excellent condition. No nymphs were seen to feed on the eggs or larvae of the ants. Some attempted to feed but apparently the eggs and larvae were too tough to be used as food by unfed nymphs.

Mite culture 106 consisted of fifteen adults that were collected with the Berlese funnel. On 21 September each one was put in an individual embryological watch glass that was coated with blackened plaster. The following day two eggs were seen in one of the watch glasses. While observing it one of the adults pierced one of the eggs and sucked it dry. After finishing the egg the adult extruded an orange sphere of material from its anus. Such spheres were found in all the cultures in which nymphs and adults were feeding on insect eggs but were not found in other cultures. Usually the spheres were white. It is assumed that they consisted of waste materials. Both of the eggs from this culture were mounted and it was found that they were both collapsed and were both covered by bits of plaster and charcoal. This indicates that they had been rolled about over the bottom of the culture dish in a manner similar to that described above.

The cultures that were fed on eggs of insects showed differences that might be attributed to the type of food provided. Nymphs and adults that fed on eggs of *Drosophila melanogaster* were light in color and resembled specimens collected in the field. Adults were seen in the four cultures that were started with unattached chiggers in from nine to thirteen days after the appearance of the nymphs. Culture 109 that fed on eggs of *Tribolium castaneum* contained healthy looking nymphs similar to those fed on the eggs of Drosophila. Two nymphs encysted to form the imagochrysalis stage six days after they had emerged from the nymphochrysalis. Six days later the first adults appeared to make a total of twelve days from the emergence of the nymph to the appearance of the adult. Cultures fed on the eggs of mosquitoes *Culex quinquefasciatus, Culex jepsoni, Aedes aegypti,* and *Aedes pandani* produced dark colored individuals. One culture fed on Aedes had adults fourteen days after the appearance of the nymphs. Adults were first seen in cultures fed on Culex eggs from fourteen to thirty days after emergence of nymphs.

Discussion

Life cycle (Fig. 17)—The life cycle of *A. indica* is similar to that of *Trombicula akamushi* and *Acariscus hominis.* Eggs laid singly are rolled about by the females. The raised ornamentation on the surface of the eggshell picks up particles of dirt and dust that apparently protect it from the adult, since if eggs are found by adults they are eaten. Females will even eat eggs that they themselves have laid. During development the eggshell splits on the sixth day to reveal a deutovum that is enclosed in a granular cuticle that contains the developing larva. Six days later the larva emerges from the deutovum. After hatching, the larva feeds on the ears of a suitable small rodent. Engorgement can be completed in as little as ten days but may be extended to as long as thirty-two days. After engorgement the chigger detaches and a nymphochrysalis develops that produces a nymph in from four to six days. The nymph feeds and in as little as six days can become quiescent. Within the quiescent nymph an imagochrysalis develops from which the adult emerges in about six days. In the culture that produced an adult in nine days after the emergence of the nymphs, the imagochrysalis was not seen, so the

relative length of time spent in the two stages is unknown. The adults are male and female. Eggs are laid by adults in as short a time as eleven days after their emergence from the imagochrysalis.

Behavior—The fact that larvae do not detach from their hosts individually but usually come off in groups is interesting. Two explanations of this phenomenon are plausible. It may be that larvae remain attached until some external factor such as light, humidity, or the activity of the host stimulates them to detach. The second explanation is suggested when examination of the tissue to which the larvae are attached is made. The damage caused by the saliva introduced into the wound made by the chiggers

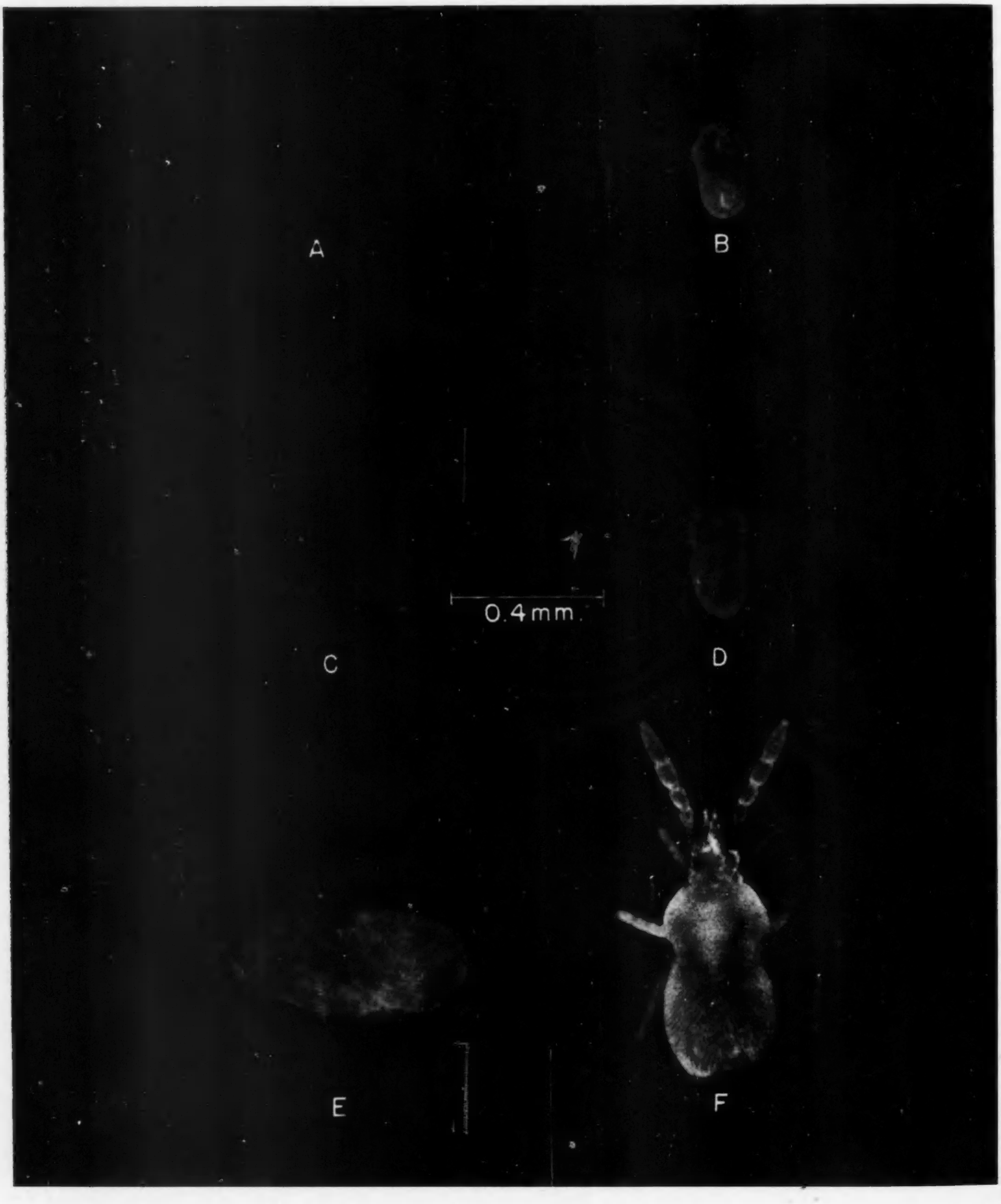

FIG. 17. Photograph of stages in life history of *A. indica.* A. eggshell and deutovum, B. larva, C. nymphochrysalis, D. nymph, E. imagochrysalis, F. adult. (Photography by Thrasher.)

causes a crust to be produced over the lesion. As further degeneration of the tissue of the host progresses this crust becomes thicker and thicker. Eventually the crust is sloughed off. Whether this occurs before or after the chiggers detach is not yet known, but if it occurs while the chiggers are still attached it would explain why they fall off in groups rather than singly. That the chiggers do drop in groups is important. Since they are dioecious it is desirable that males and females develop in the vicinity of each other.

The appearance of spherical particles of waste material associated with all the active stages in the life of *A. indica* has a bearing on an important and disputed point in their anatomy and physiology. Blauvelt 1945 in discussing *Tetranychus bimaculatus* Harvey discovered that in this species the mid- and hind-gut were connected, and feces were thus voided through the anus. Up until Blauvelt's study the concensus of opinion favored the view that mid- and hind-gut were unconnected in all of the Prostigmata, and that the hind gut functioned solely as an excretory organ. The observation that spherical pellets of waste material were seen associated only with completely engorged larvae, and with nymphs and adults only after they had fed, suggests that the mid-gut opens into the hind-gut of *A. indica.*

Copulation and egg-laying were not observed. It is highly probable that initial stages of copulation proceed as described under mite culture 101. That copulation does occur seems certain from the study of the genital openings and the relative frequency of males and females.

OBSERVATIONS IN THE FIELD

Introduction

Guam is at the southern tip of the Marianas Islands. It is situated at 13° 30′ north latitude and 144° 45′ east longitude in the central portion of the Pacific Ocean. The island is roughly banana-shaped and its long axis extends for thirty miles from north to south. The northern half consists of a plateau that is about five hundred feet above sea level. The sides of the plateau rise abruptly from the sea so that much of the coast line presents a perpendicular coral cliff to the open sea. The southern half of the island has a much more irregular terrain and the soil is largely volcanic in origin. Several rivers are on the southern half of the island that run from the center of the island to the coast. On the northern half of the island most of the water percolates through the porous coral rock.

Safford 1905 discusses the vegetation on Guam in his book on the useful plants. Along the beach there are many coconut groves and in some areas mangrove swamps. At the northern half of the island a typical tropical rain forest covers the tops of the coral cliffs. Much of the interior of the plateau is covered by stands of tall grass or has been in cultivation. At the time that this study was conducted most of the original cover had been destroyed by the installation of numerous military activities. The northern half of the island was transformed into a huge military base consisting of many units of all branches of the service. The southern half was relatively unoccupied by our armed forces, but much of the native population was concentrated in this area. Most of the hills that had a red volcanic soil were covered with tall grass, while areas with sedimentary soil were used for agriculture by the natives.

Materials and Methods

Hosts—Collections of vertebrates were made largely by the laboratory of mammalogy. A routine was established whereby vertebrates were placed in refrigerators as soon as they were brought in from the field. The specimens were then examined for ectoparasites before being returned to mammalogy for study and preservation. Most of the vertebrates collected were preserved and are now in the custody of the U. S. National Museum. Ectoparasites were preserved by dropping them into eighty-five per cent alcohol. Many of them were subsequently mounted in appropriate media for study and identification.

Arthropods—Collections of free-living trombiculids and the numerous small arthropods associated with them were greatly facilitated by the use of Berlese funnels. Debris to be examined was collected in the field in bags of appropriate size. When these were brought into the laboratory they were stored in large photographic trays until examination was made. Samples of material about a half liter in volume were wrapped in a double thickness of cheese cloth and placed in Berlese funnels. The samples remained in the funnels until they were completely desiccated. The time required to desiccate the debris varied from four to more than forty-eight hours. Specimens were collected in water-filled jars that were placed under each of the funnels. A battery of six funnels was used. Specimens were removed from the surface of the water in the jars and preserved in eighty-five per cent alcohol or were placed in culture bottles for further study in the laboratory.

Results

Trombiculid mites—Ten species of chiggers were collected. Of these only one species, *A. indica,* was found on a mammal, *Rattus mindanensis.* The other nine species occurred on birds. One species was also found on a monitor lizard. Two of them, *Trombicula acuscutellaris* Walch 1922 and a new sub-species of *Neoschöngastia americana* (Hirst 1921) were previously known. The other seven species were new and have been or will be described elsewhere. The collection records of chiggers other than *A. indica* are given in Table 3. No nymphal or adult trombiculids except *A. indica* were collected. No chiggers were found on man.

Hosts—*A. indica* has been found only on small mammals. Since the only small mammals on Guam are murid rodents the discussion of hosts will be confined to the three native species found in relatively

large numbers throughout the island. Baker (manuscript in preparation) discusses the ecology of murid rodents on Guam.

Mus musculus was captured at many localities. In all eighty-eight specimens were examined for chiggers and all were found to be negative. *Echinolaelaps echidninus* (Berlese) and *Laelaps nuttali* Hirst were occasionally found on mice. Mice were rare in the rain forest but were fairly common in and around certain villages and open grassy areas (Fig. 18). Thirty-seven of the specimens examined were collected at Sinajana Village.

FIG. 18. View of grass covered area near Mt. Santa Rosa. Rodents living in such areas are not infested with *A. indica*. (Photography by Poe.)

TABLE 3. Hosts of species of chiggers other than *Ascoschöngastia indica* collected on Guam.

Acariscus pluvius Wharton 1945
- *Anous stolidus*—Noddy tern
- *Numenius phaeopus*—Whimbrel
- *Heteroscelus incanus*—Wandering tattler
- *Pluvialis dominica*—Golden plover

Acariscus anous Wharton 1945
- *Anous stolidus*—Noddy tern
- *Numenius phaeopus*—Whimbrel
- *Heteroscelus incanus*—Wandering tattler
- *Pluvialis dominica*—Golden plover
- *Arenaria interpres*—Turnstone

Trombicula acuscutellaris Walch 1922
- *Ixobrychus sinensis*—Least bittern

Trombicula n. sp. Will be described by Womersley
- *Corvus kubaryi*—Guam crow
- *Rhipidura rufifrons*—Fantail flycatcher
- *Aplonis opacus*—Starling
- *Halcyon cinnamomina*—Kingfisher
- *Gallicolumba xanthonura*—Ground dove
- *Streptopelia bitorquata*—Turtle dove
- *Varanus indicus*—Monitor lizard

Neoschöngastia americana solomonis Wharton and Hardcastle in press
- *Anous stolidus*—Noddy tern

Neoschöngastia bougainvillensis Wharton and Hardcastle in press
- *Anous stolidus*—Noddy tern
- *Heteroscelus incanus*—Wandering tattler

Neoschöngastia ewingi Wharton and Hardcastle in press
- *Heteroscelus incanus*—Wandering tattler

Neoschöngastia carveri Wharton and Hardcastle in press
- *Numenius phaeopus*—Whimbrel
- *Demigretta sacra*—Reef heron
- *Pluvialis dominica*—Golden plover
- *Arenaria interpres*—Turnstone

Neoschöngastia namrui Wharton and Hardcastle in press
- *Numenius phaeopus*—Whimbrel
- *Heteroscelus incanus*—Wandering tattler
- *Pluvialis dominica*—Golden Plover

Neoschöngastia strongi Wharton and Hardcastle in press
- *Numenius phaeopus*—Whimbrel

Rattus exulans the so-called Polynesian rat is frequently associated with native gardens and altered jungle on islands throughout the central and western Pacific Ocean. On Guam this species had much the same habits as *Mus musculus* except that it was not found in close association with native houses or military installations. Sixty specimens were examined for chiggers and all were negative. *Echinolaelaps echidninus* and *Laelaps nuttali* were found.

A species of Rattus that belongs to the *Rattus rattus* group and which has been tentatively identified as *Rattus mindanensis* proved to be the sole host of *A. indica* on Guam. It was also parasitized by *Echinolaelaps echidninus* and *Laelaps nutalli*. A study of this rat was made in the field at Oca Point where it was most heavily infested with *A. indica*. Baker studied it extensively in the Mount Santa Rosa area.

U. S. Naval Medical Research Unit No. 2 was established on Oca Point in an area that had been virgin rain forest (Figure 19). The forest was removed just prior to the construction of the unit, and rats that formerly inhabited it found new quarters in the piles of brush and trees that surrounded the cleared area, in the supply dump, and in and under the buildings. A thorough poisoning campaign removed most of the rats from the cleared area, but continued poisoning was necessary to prevent rats from adjacent areas from reestablishing themselves.

The first nest of *Rattus mindanensis* to be discovered was found under a pile of lumber in the supply dump by men who were moving lumber. It was made of shredded debris, including newspaper. The nest was not buried in the ground. The walls and floor were excavated, but the roof was covered only by lumber. Examination of areas in the rain forest for nests in natural surroundings was then made. Habitats considered to be similar to that afforded by the lumber pile were investigated. It was soon found that accumulations of the fruits of *Ochrosia mariannensis* were located at the openings of tunnels in coral cliffs and under the roots of stumps and trees (Fig. 20). Rats were seen in some of these localities, and thus it was assumed that piles of *Ochrosia*

FIG. 19. View of rain forest at Oca Point. *Rattus mindanensis* here was heavily infested with *A. indica*. (Photography by Poe.)

mariannensis fruits could be used as indicators for the locations of the hiding places of rats. These hiding places were frequently found in the soil-like bases of clumps of epiphytic ferns that were abundant on large trees (Fig. 21). *Ochrosia mariannensis* fruits were found in a nest that was made of leaves that had not yet lost their green color. Marks on these fruits were assumed to have been made by the teeth of *Rattus mindanensis* (Fig. 22). Comparison of the marks with tooth marks of *Rattus mindanensis* kept in the laboratory confirmed the above assumption.

FIG. 20. Entrance to nest of *Rattus mindanensis* under a log on Oca Point. (Photography by Poe.)

One hundred and sixty-three specimens of *Rattus mindanensis* were obtained from Lieutenant W. G. Crabb, the Island Rodent Control Officer. These had been collected by the natives of Agat village at the termination of a poisoning program and were either dead or dying when delivered for examination. Agat village is on a sandy beach near the southern end of the island. It is composed of about a hundred frame houses that have heavily thatched roofs. Conversation with natives of the village revealed that most of the rats had been living in the thatched roofs. They also stated that the rats were inactive during the day, but were active at night and were frequently seen and more frequently heard in the roofs after dusk.

Distribution of A. indica *on Guam* (Fig. 23)—The distribution of attached larvae is conditioned by the distribution of their host *Rattus mindanensis*. Table 4 gives in detail the distribution of *Rattus mindanensis* as well as of chiggers of *A. indica*. Figure 23 shows the location of collection sites. Collections of nymphs and adults were made only at Oca Point.

Although *Rattus mindanensis* occurred over most of the island *A. indica* was collected primarily from rats captured along the western coast. No ready explanation is available for the sporadic distribution. It is similar to the distribution of other species. Chiggers are seldom uniformly distributed over an area but seem to be restricted to certain types of habitats. On Guam *A. indica* was found abundantly in the rain forest that tops the abrupt coral cliffs. It also occurred in the coconut groves that abutted the beaches at Agana, Tumon Bay, and Tarofofo Bay. It was not found in grassy upland areas such as occurred near Mount Santa Rosa (Fig. 18). The type of vegetation however was not the only factor in the distribution of *A. indica* since rats collected in the rain forest at Ritidion and Patay Points were not infested while the highest infestation occurred

FIG. 21. Epiphytic fern. Most ferns on Oca Point contained nests of *Rattus mindanensis*. (Photography by Poe.)

FIG. 22. Fruits of *Ochrosia mariannensis* that have been partially consumed by *Rattus mindanensis*. (Photography by Poe.)

in the vicinity of Oca Point where conditions were similar to the former areas.

Collections of free-living A. indica—Nymphs and adults of *A. indica* were first found in nature by Radford 1946 in the debris at the tops of coconut trees. On Guam they were first found in a collection of material from a rat's nest. The nest (Fig. 24)

TABLE 4. Collections of *Rattus mindanensis*.

Locality	Number Examined	Positive for *A. indica*	Negative for *A. indica*
1. Oca Pt.	190	156	34
2. Ypao Pt.	4	4	0
3. Tumun Bay	24	11	13
4. Amantes Pt.	5	1	4
5. Ritidion Pt.	12	0	12
6. Patay Pt.	5	0	5
7. Mt. Santa Rosa	17	0	17
8. Yigo	30	0	30
9. Sinajana	4	0	4
10. Tarafofo	15	6	9
11. Merizo	8	0	8
12. Agat	164	5	159
13. Sumay	6	0	6
14. Piti	66	31	35
15. Anigua Pt.	25	10	15
16. Agana	6	2	4

was in a soil-like concentration of debris gathered and held together by the roots of epiphytic ferns. The fern had fallen from its original position on a nearby Ochrosia tree and was lying in a tangle of Pandanus stumps. The root system of the fern was approximately three feet in diameter and contained three passageways and two excavations that were evidently used as nests or resting places by *Rattus mindanensis*. No *Rattus exulans* were discovered in the general area in which the nest was found. The excavations in the root system were lined with dried leaves of cycads and *Ochrosia mariannensis*. The tunnels or passageways connecting the two nests were one to one and a half inches in diameter.

Material from the nests were put into a Berlese funnel. Four males, one female, and one nymph of *A. indica* were collected from this material. Other small arthropods were also collected. Most of these could not be determined specifically because they belonged to obscure groups which have not yet been sufficiently studied. Five species of mites were found: one unidentified mesostigmatan, *Echinolaelaps echidninus*, *Cosmolaelaps sp.*, *Laelaps sp.*, and *Eupodes sp.* Nine species of insects were also found: three lepidopterans two of which belong to the Tineidae while the other is probably an oecophorid, two species of staphalinid beetles *Medon sp.* and *Gyrphaena*, three species of ants *Anoplolepis longipes*, *Strumigenys membranifera*, and *Ponera sp.* and one collembolan *Lepidocyrtus sp.*

Examination of material from the mass of roots and soil that surrounded the nests yielded one female of *A. indica* and in addition other small arthropods including five species of mites, a collembolan *Lepidocyrtus sp.* and a spider *Tetrablemma sp.* The mites were: *Tyrophagus sp.*, *Tyrophagus putrescentae*, *Hypoaspis sp.*, *Cosmolaelaps sp.*, and an unidentified mesostigmatan.

Investigation of seven rats' nests found in or near the ground yielded no specimens of *A. indica*, but *A. indica* was found in material from a hole in the ground under a log and in debris collected from a nest in a hollow log. Three collections were made of

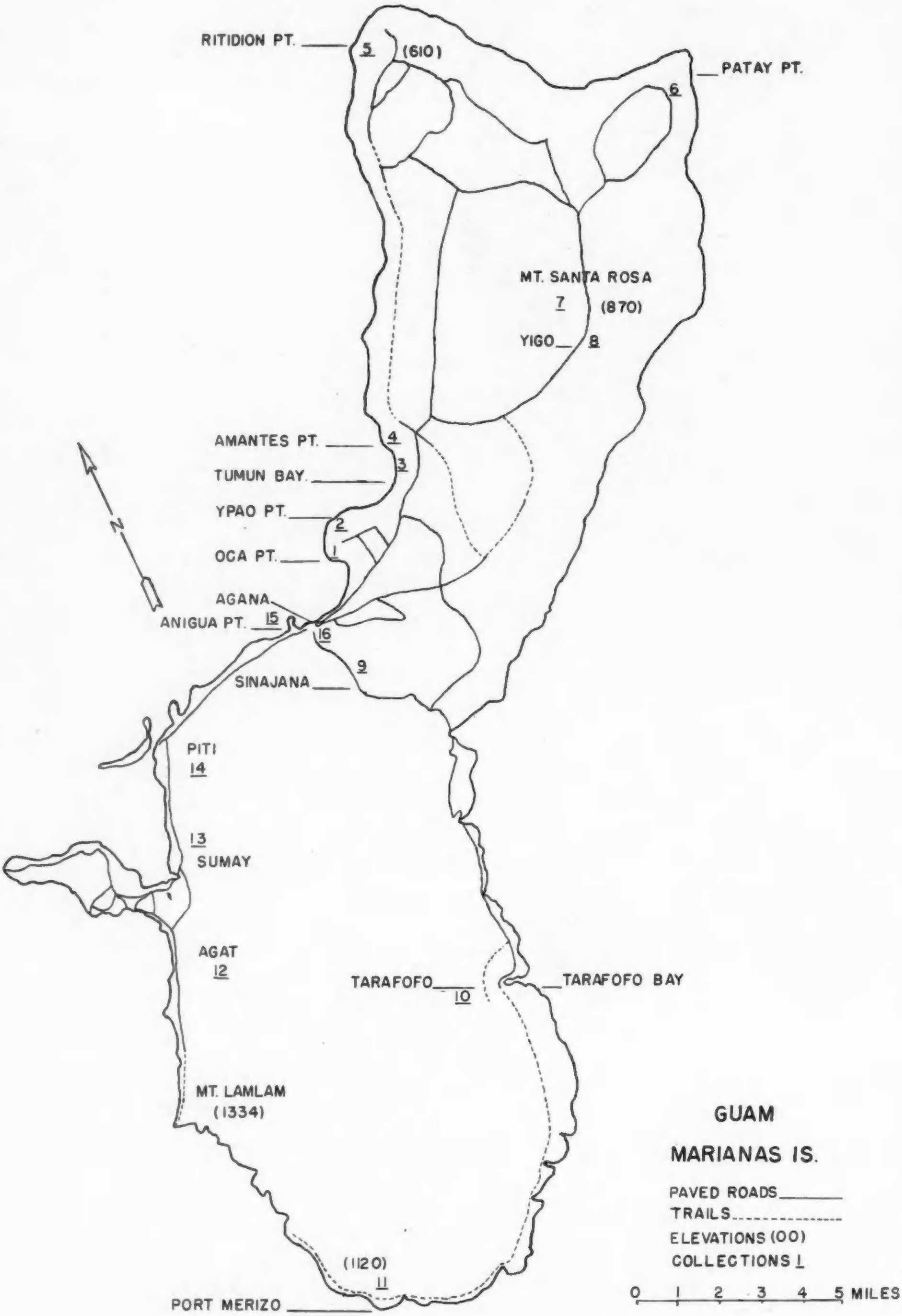

FIG. 23. Map of Guam. (Drawn by Carver.)

FIG. 24. Nest of *Rattus mindanensis* in an epiphytic fern. (Photography by Poe.)

debris on the ground not adjacent to the nests or runways of rats. These were all negative for *A. indica*. Debris that had collected in the forks of two trees was put in the Berlese funnels. No specimens of *A. indica* were found in this material. Five rats' nests found in epiphytic ferns were investigated as well as four ferns which contained no evidence of nests. *A. indica* was found in four of the five nests and was not found in the four ferns that contained no nests.

In contrast to most mites, males were found more frequently than females. In one of the few collections from which adults of *A. indica* were prepared for study there were thirty-six males, seventeen females, and forty nymphs. Of the females, nine contained eggs. Usually more than a single egg was present at one time but in no case were there more than two mature eggs.

Arthropods associated with A. indica—Since it was discovered that *A. indica* used the eggs and early larval instars of small arthropods as food, a collection of these was presented to the Division of Insect Identification of the Department of Agriculture for identification. Free-living mites were also identified as far as they could be readily determined. Specimens of the following arthropods were found associated with habitats from which *A. indica* was taken or from similar accumulations of debris.

Phylum—Arthropoda
Subphylum—Chelicerata
Class—Arachnidea

Order—Chelonethida—Pseudoscorpions are small arachnids with enlarged chelate pedipalps. They are predacious and probably live on the other small arthropods associated with them. Their eggs may be protected by a web and so may not be available as food for nymphs and adults of *A. indica*. Determinations were made by J. C. Chamberlain.

Tyrannochthonius n. sp.
Oratemnus bötcheri Beier
Pycnochernes (?) *n. sp.*

Order—Acarinida—Mites other than *A. indica* were found in abundance. The mites are diverse in their habits and no general statement can be made concerning their food habits and egg-laying. Assistance in identification of the mites was received from E. W. Baker.

Suborder—
Mesostigmatina
Gamasiphis sp.
Macrocheles sp.

Asca magnituberculatus (Vitzthum) New combination
Cosmolaelaps 2 *sp.*
Seiulus sp.
Hypoaspis sp.
Laelaps nuttali Hirst
Echinolaelaps echidninus (Berlese)
Rhodacarus sp.
Epicrius sp.
Euzercon ovulum Berlese
Uropoda sp.

Plus several species that were represented only by males or immature stages and so cannot be placed generically and two species that probably represent new genera.

Suborder—
Trombidina
Raphignathus sp.
Proteroneutes sp.
Ereynetes sp.
Opsereynetes sp.
Eupodes sp.
Becksteinia sp.
Rhagidia sp.
Linopodes sp.
Bimichaelia sp.
Bdella sp.
Scirus longirostris (Herman)
Tetranychus sp.
Eupalus sp.
Cunaxa simplex Ewing
Cheyletus malaccensis Oudemans
Variatipes sp.

Suborder—
Sarcoptina
Tyrophagus putrescentiae (Schrank)
Tyrophagus lintneri (Osborne)
Caloglyphus sp.

Plus several unidentified species of the cohort Orabatina.

Order—Araneida—Small spiders were frequently found. Spiders are predacious and usually although not invariably lay their eggs in cocoons. All spiders were determined by H. H. Swift.
(Oonopinus sp. ?)
Tetrablemma sp.
Opopaea sp.

Subplylum—Mandibulata
Class—Insectea
Subclass—Apterygotia

Order—Thysanurida—An undetermined species of the subfamily Nicoletiinae was reported by G. Glance who also studied specimens of the next two orders. All of the Apterygotia collected are probably herbaceous and probably represent an important source of food for the predacious species. Whether their eggs are suitable for *A. indica* or not is unknown.

Order—
Entotrophida
Lepidocampa sp.

Order—
Collembollida
Lepidocyrtus sp. (The most common springtail found in the collections and probably the one used in the cultures.)
Entomobrya sp.
Proisotoma sp.
Sinella sp.
Seira sp.

Subclass—Pterygotia

Order—Blattida—Specimens of this and the next two orders were determined by H. Townes.
Pycnoscelus surinamensis (L.)

Order—
Corrodentida
Psocidae, genus ?

Order—
Dermapterida
Euborellia annulipes (Lucas)

Order—Homopterida—Determined by R. I. Sailer.
Ceratocombus sp.
Cligenes (?) *sp.*
Geotomus pygmaeus (Dallas)

Order—Coleopterida—Many of the beetles found were herbivorous. Since *A. indica* can develop satisfactorily on the eggs of *Tribolium castaneum* it is reasonable to suppose that eggs of the numerous beetles found associated with it in the field may be an important source of food.
Medon sp.
Pseudolispinodes sp.
Aleocharinae, genus ?
(Determined by R. E. Blackwelder)
Ptiliidae—two species belonging to undetermined genera.
One species belonging either to the Staphylinidae or Pselaphidae.
Acritus sp.
(Determined by H. S. Barber)
Haptoncus sp.
Carpophilus sp.
(Determined by E. A. Chapin)
Choerorrhinodes constricticeps Zimmerman
Noterophagus sp.
(Determined by L. L. Buchanan)
Endomychidae, genus?
Gyrophaena sp.
Eumicrus sp.
(Determined by B. E. Rees)

Order—Lepidopterida—Larvae of four families were collected. These were determined by C. Heinrich as follows: Tineidae, Oecophoridae (?), Pyralididae, and Pyraustidae.

Order—Dipterida—Several larvae were collected. Eggs of Drosophila and mosquitoes were found to be satisfactory food for *A. indica*.
Discocerina sp. (Determined by D. G. Hall)
Lycoria sp. (Determined by A. Stone)
Psychodidae, genus?
Drosophila sp.
Desmometopa sp.

Chrysops ? sp.
Psychodidae?
Itonidae, genus?
(Determined by C. T. Greene)
Chonocephalus n. sp. (Determined by G. E. Bohart)

Order—Hymenopterida—Only ants were found. Eggs and first instar larvae of *Anoplolepis longipes* were used as food by *A. indica* in the laboratory. Ant eggs that are guarded by the workers of a colony in nature may not be available to *A. indica*. M. R. Smith determined the ants.

Anoplolepis longipes (Jerd.)
Strumigenys membranifera Emery, broad sense.
Strumigenys godeffroyi Mayr
Ponera sp.
Pheidole umbonata Mayr
Paratrechina minutula atomus fullawayi Wheeler
Paratrechina bourbonica Forel
Triglyphothrix striatidens Emery
Monomorium floricola (Jerd.)
Epitritus sp.
Camponotus sp.
Solenopsis geminata rufa (Jerd.)

Discussion

Observations made in the field are consistent with those made in the laboratory. Only *Rattus mindanensis* was found to harbor chiggers of *A. indica*. One plausible explanation of the absence of *A. indica* on *Mus musculus* and *Rattus exulans* is that these species were rare or absent from the rain forest where *Rattus mindanensis* was most heavily infested. *Rattus mindanensis* itself was not infested in areas where *Mus musculus* and *Rattus exulans* were most abundant. *Rattus mindanensis* has frequently been found to be arboreal, and the free-living stages of *A. indica* were found more frequently in rats' nests that were excavated in epiphytic ferns than they were in those made on the ground.

Eggs and early larval instars of many of the small arthropods that were found to be associated with *A. indica* in the field probably comprise its supply of food.

SUMMARY AND CONCLUSIONS

Distribution—Ascoschöngastia indica has been recorded from Calcutta, India; Deli, Sumatra; Southern Sumatra; Macasser, Celebes; Federated Malay States; Cairns, Queensland; Batavia, Java; Colombo and Embeliptiya, Ceylon; Maldive Islands; Manila, Lyngayen, Bagabag, and Mabitae, Luzon; Burma;[1] and Guam. In all of these localities it was found to be parasitic on small rodents. While in many cases the host is listed as "rats," it has been recorded from the following species: *Bandicota bengalensis*, *Rattus rattus*, *Rattus concolor*, *Rattus sabanus*, *Rattus canus*, *Rattus norvegicus*, and *Rattus mindanensis*. On Guam *A. indica* was found to be present on *Rattus mindanensis* but only in restricted localities.

[1] Unpublished record from the U. S. Typhus Commission.

The geographical distribution of *A. indica* is typical of many other species of Trombiculidae. It is present in restricted localities over a large geographical area. There are two phases in the habits of trombiculid mites that condition their geographical spread. The parasitic phase during the larval stage can be considered as an adaptation for dispersal of the species. If this conclusion is correct, then a consideration of the dispersal of hosts is important in discussing the geographical range of trombiculid mites. Rats are readily transported from one locality to another as is evidenced by their wide distribution on isolated islands in the Pacific. Larvae of *A. indica* are known to remain on the host for more than thirty-two days. It is therefore possible that *A. indica* was introduced throughout its range with the rodents that it parasitizes. The free-living phase of trombiculid mites in which are included all stages from the detached engorged larva through the nymph, adult, egg, and unattached larva can be thought of as determining the local distribution of a trombiculid. Trombiculid mites are characteristically restricted in the free-living stages by type of cover, temperature, humidity, light, and other factors. *A. indica* was first found in its free-living phase in the tops of coconut palms but on Guam was restricted to runways, nests, and hiding places of *Rattus mindanensis* that were protected by some type of cover. Nymphs and adults were more frequently found in such localities in epiphytic ferns that occur high in the branches of the trees in the rain forest than they were on or near the ground. It is possible that the free-living phase of *A. indica* is usually arboreal because accumulations of water do not remain as long in the trees as they sometimes do on the ground.

It is unusual for trombiculid mites to show a definite host specificity. Usually when specificity is shown it is a matter of spatial rather than specific relationships. Some trombiculids may parasitize many species in all classes of terrestrial vertebrates. *A. indica* is exceptional in that it has been found only on small rodents. On Guam it was found to parasitize only *Rattus mindanensis*. Part of its host specificity can be readily explained on the basis of spatial relationships. *Mus musculus* and *Rattus exulans* two small rodents that are common on Guam do not regularly climb trees, but are more or less confined to grassy areas where even *Rattus mindanensis* does not become infested with *A. indica*. The fact that *A. indica* is found only in the covered runways and nests of *Rattus mindanensis* also explains why it has not been found on other vertebrates. In other words many animals are free from the attacks of *A. indica* because they do not wander into the restricted habitats in which the unattached larvae of *A. indica* are found. However this is not the complete explanation since attempts to infest *Rattus exulans*, *Mus musculus*, Guinea pigs, and chickens were all negative while some of those made to infest *Rattus mindanensis* were positive. It should be emphasized however that *A. indica* has been found in Asia on

Rattus concolor, a species that is closely related to *Rattus exulans.*

In conclusion it is suggested that the geographical range of trombiculid mites is largely dependent on the geographical range of their hosts; the local distribution is conditioned by the behavior and habits of the free-living stages, and the host distribution is conditioned by the habits of the hosts as well as specific peculiarities of both host and parasite.

Morphology and development—The egg of *A. indica* is similar to that of *Acariscus hominis* as described by Michener. The chorion is ornamented by raised areas in *A. indica* while depressed areas are mentioned in Michener's account. The main difference in ornamentation is that in *A. indica* the raised areas are discontinuous while in *Acariscus hominis* the raised areas are continuous.

A deutovum is known from the three species of trombiculids whose life histories are completely known. This stage in the development of the larva is similar to the chrysalis stages in the development of nymphs and adults. As the development proceeds in the egg the general body form is laid down and a sclerotized membrane develops about the embryo. The appendages have appeared but are not yet differentiated. It is within the deutovum that the larva differentiates. A similar stage appears in the transformations from larva to nymph and from nymph to imago. In the formation of the nymph or the imago, the appendages of the preceding stage undergo histolysis and all of the cells of the appendages become indifferent. In other words a condition similar to that of the deutovum is produced and a membrane is formed around this indifferent stage similar to that surrounding the deutovum. The eggshell splits exposing the deutovum, but the skin of the preceding stage always encloses the chrysalis. Some confusion has arisen concerning the proper designation of these various stages. Michener 1946 uses deutovum, protonymph, and preadult. The term protonymph is used for the first active nymphal stadium in other mites and cannot properly be used for a quiescent organism. Therefore the term nymphochrysalis as used by Miyajima & Okumura 1917 is used. Since the nymph passes through a similar stage in going to the adult or imago this stage can be logically called an imagochrysalis. The term deutovum is maintained because while the stage is similar to both nymphochrysalis and imagochrysalis it is also homologous to the deutova of other arachnids. The skin that covers these intermediate stages is here designated as a secondary cuticle to distinguish it from the primary cuticle of the preceding stage.

The morphology of the active stages of *A. indica* has been described in detail. Larva, nymph, and adult are similar to those of other members of the family. The genital openings have been carefully described and secondary sexual characters that differentiate males from females have been discovered on the genital plates. The male has a pair of large specialized setae and more numerous generalized setae than are found on the female. No sexual differences could be found in any stages other than the adult. Michener 1946 points out that imagochrysalises of males are smaller than those of the females of *Acariscus hominis.* He does not mention how he determined the sex of the imagochrysalis but probably the developing imago contained in it could be sexed.

The life cycle of *A. indica* can be summarized as follows: eggs are laid by the females, eggs are 150 microns in diameter and develop in six days to the deutoval stage; deutova are 180 microns in length and contain the differentiating larvae which hatch in six days; the unattached larvae average 185 microns in length, they attach to small rodents and may engorge for as long as thirty-two days, when fully engorged they may attain a length of 394 microns, after detachment the engorged larvae enter a quiescent stage; nymphochrysalises develop within the larval skins, they are about 400 microns long, in from four to six days nymphs emerge from them; nymphs feed on insect eggs and average 480 microns in length. They can become quiescent in as little as six days; imagochrysalises develop within the nymphal skins, they are about 750 microns in length, adults or imagos emerge from them in six days; the adults are male and female, males average 647 microns in length, while females average 662 microns, adults can live for at least three months and probably longer, they also feed on insect eggs.

Habits—Most trombiculid mites that have been studied live in the soil during their free-living existence. *A. indica* is unusual in that it is largely arboreal, living in the soil-like accumulations of debris at the tops of coconut trees (Radford 1946) or in rats' nests in epiphytic ferns.

The larvae are similar in habits to other trombiculids. They occur in groups in the ears of rats where they secrete saliva into the tissue. The saliva digests the tissue and also forms a feeding tube through which the larvae suck up the digested tissue and lymph of the host. No blood is used as food.

The food habits of nymphs and adults of *A. indica* are different from those reported for other trombiculid mites. However the actual source of nutriment for other trombiculids is still unknown. Michener 1946 and Melvin 1946 used chicken dung as food but although nymphs developed into adults Michener states that the actual food of the species on which he worked is still unknown. His guess is that fluid from chicken dung is used. Ewing (1944) reared *Eutrombicula alfreddugèsi* on feces of small arthropods. He was able to get only a few adults from many nymphs. This indicates that the food was not readily available to the mites and not entirely satisfactory. Similar results were obtained by Japanese workers who studied *Trombicula akamushi.* Miyajima and Okumura used fruit as food. *A. indica* on the other hand developed normally on insect eggs in the laboratory and lives in association with many small arthropods in nature whose eggs and early larval instars probably comprise its food.

A. indica lays eggs singly. Recently Melvin 1946 reported that species of Acariscus may lay their eggs in clumps of as many as fifty-six. Michener 1946 working with the same species found that the eggs were laid singly. *A. indica* rolls its egg about after it has been laid so that it picks up debris for its protection. Unless the eggs of *A. indica* are disguised they will be eaten. This type of behavior is not known for other species.

Cultures—No entirely satisfactory system for culturing trombiculid mites has yet been described. Melvin 1946 reports carrying mites through more than two generations by the use of "mass" culture methods. He is the first to report such success on any species. No indication of the regularity with which his method produces results is given. The system described by Michener is a modification of Melvin's methods. Michener does not indicate how many generations he was able to rear or whether he was able to increase the number of individuals in each successive generation. The method described here for *A. indica* is satisfactory for producing nymphs and later adults from engorged larvae. While a few eggs and chiggers were obtained more satisfactory methods must be developed to increase the yield of chiggers if successful culturing is to be achieved. A system of feeding unattached chiggers on a suitable host was described by Michener 1946. The method used for *A. indica* described in this paper was unsatisfactory because so few engorged chiggers were recovered. Michener 1946 gives no indication of how many chiggers were recovered when his system was used. The work of Michener and Melvin and that reported in this paper indicates that satisfactory methods for culturing trombiculid mites can be developed. The most difficult problem, that of providing food for the free-living stages, has been solved.

REFERENCES

André, M. 1930. Contribution a l'etude d'un acarien: le Thrombicula autumnalis Shaw. Mem. Soc. Zool. France **29**: 39-138.

1938. Quelques observations sur la larve de Thrombicula autumnalis Shaw a l'etat de vie libre. Bull. Soc. Zool. France **63**: 45-47.

Blauvelt, W. E. 1945. The internal morphology of the common red spider mite (Tetranychus telarius Linn.) Cornell Agric. Exp. Sta. Mem. **270**: 1-35.

Ewing, H. E. 1926. The life history and biology of the tree-toad chigger, Trombicula hylae Ewing. Ann. Ent. Soc. Amer. **19**: 261-267.

1929. A manual of external parasites. Baltimore 225 + XV.

1944. The trombiculid mites (chigger mites) and their relation to disease. J. Parisitol. **30**: 339-365.

1946. Notes on the taxonomy of three genera of trombiculid mites (chigger mites), together with the description of a new genus. Proc. Biol. Soc. Wash. **59**: 69-71.

1946a. Taxonomic notes on American chiggers (larvae of the mite family Trombiculidae), including the redescription of a genus and the descriptions of two new species. Proc. Biol. Soc. Wash. **59**: 21-28.

Fletcher, W., J. E. Lesslar, & R. Lewthwaite. 1928. The aetiology of tsutsugamushi disease and tropical typhus in the Federated Malay States. Trans. Soc. Trop. Med. Hyg. Lond. **22**: 161-174.

Gater, B. A. R. 1932. Malayan trombidiid larvae, Part 1 (Acarina: Trombidiidae) with descriptions of seventeen new species. Parasitol. **24**: 143-174.

Gunther, C. E. M. 1939. Observations on the life history of Neoschöngastia kallipygos Gunther 1939. (Acarina: Trombidiidae). Proc. Linn. Soc. New South Wales **64**: 471-473.

1941. Studies in Trombidiidae (Acarina: Trombidiidae). Proc. Linn. Soc. New South Wales **66**: 391-395.

Hirst, S. 1915. On some new acarine parasites of rats. Bull. Ent. Res. **6**: 183-190.

Keay, G. 1937. The ecology of the harvest mite (Trombicula autumnalis) in the British Isles. Ecology **6**: 23-35.

Melvin, R. 1946. A note on the culturing of chiggers (Trombiculidae). Ann. Ent. Soc. Amer. **49**: 143-144.

Michener, C. D. 1946. Observations on the habits and life history of a chigger mite, Eutrombicula batatas (Acarina: Trombiculinae). Ann. Ent. Soc. Amer. **49**: 101-118.

Miyajima, M., & T. Okumura. 1917. On the life cycle of the "akamushi" carrier of Nippon river fever. Kitasato Arch. Exper. Med. **1**: 1-14.

Philip, C. B., & P. E. Woodward. 1946. Tsutsugamushi disease (scrub or mite-borne typhus) in the Philippine Islands during American re-occupation in 1944-45.

II. Observations on trombiculid mites. Am. J. Trop. Med.

Radford, C. D. 1942. The larval Trombiculinae (Acarina, Trombidiidae) with descriptions of twelve new species. Parasitol. **34**: 55-81.

1946. Larval and nymphal mites (Acarina: Trombiculidae) from Ceylon and the Maldive Islands. Parasitol. **37**: 46-54.

Safford, W. E. 1905. The useful plants of Guam. Bull. U. S. Nat. Mus. **9**: 1-416.

Severin, H. C. 1944. The grasshopper mite Eutrombidium trigonum (Herman) an important enemy of grasshoppers. Tech. Bull. Agric. Exp. Sta. South Dakota State College **3**: 1-36.

Walch, E. W. 1922. Over T. deliensis, vermoedelijk overbrengster der pseudotyphus, en andere Delische Trombiculae. Geneesk. Tijdschr. voor Ned-Indie **62**: 530.

1923. On Trombicula deliensis, probably carrier of the pseudotyphus and on other Trombicula species of Deli. Kitasato Arch. Exp. Med. **5**: 63-83.

1924. Over de Trombiculae, welke pseudotyphus overbrengen, en na verwante mijten vit deli. Geneesk. Tijdschr. voor Ned-Indie **64**: 499-529.

1927. Nederlandsch-Indische Trombiculae en verwante mijten. Geneesk. Tijdschr. voor Ned-Indie **67:** 1-12.

Wharton, G. W. 1938. Acarina of Yucatan Caves. Carnegie Inst. Wash. Pub. **491:** 137-152.

1945. Trombicula frittsi n. sp. (Acarinida: Trombiculidae) J. of Parasitol. **31:** 282-283.

The Vectors of tsutsugamushi disease. Proc. Ent. Soc. Wash., in press.

Wharton, G. W., & R. K. Carver. Food of nymphs and adults of Neoschöngastia indica (Hirst 1915) (Trombiculidae: Acarinida). Science **104:** 76-77.

Womersley, H. 1939. Further notes on the Australian Trombidiidae with descriptions of new species. Trans. Roy. Soc. South Australia **63:** 149-166.

Womersley, H., & W. G. Heaslip. 1943. The Trombiculinae (Acarina) or itch mites of the Austro-Malayan and Oriental regions. Trans. Roy. Soc. South Australia **67:** 68-142.

MARINE ECOLOGICAL STUDIES ON SANTA CRUZ ISLAND, CALIFORNIA

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MARINE ECOLOGICAL STUDIES ON SANTA CRUZ ISLAND, CALIFORNIA

INTRODUCTION

The northern group of Channel Islands of California, namely Anacapa, Santa Cruz, Santa Rosa, and San Miguel, have long been considered to lie in an area of transition between the northern and southern California shore faunas. Several investigators including Dana (1853), Dall (1909), (1921), J. P. Smith (1919), and Bartsch (1921) have noted distinct variations in the coastal faunas found to the north of Point Conception and those ranging to the south of that area. Steinbeck & Ricketts (1941, p. 302) consider Point Conception as the northern limit of the "Panamic Province" and the southern limit of the "North temperate fauna."

By biometrical analysis of the distribution of mollusks along the West Coast Schenck & Keen (1936) found no significant break in the distribution of recent species in the region of Point Conception. Their studies included the ranges of 1948 species of pelecypods, gastropods and scaphopods without regard to bathymetric distribution. These authors do note (p. 931) that "if shore collections or shallow dredgings alone were considered, a fairly sharp line of division would appear in the vicinity of Point Conception." They presented no data, however, to support this view.

The littoral and shallow water organisms of the northern Channel Islands which lie in the overlap area have received little or no attention from marine zoologists. The writer had spent several years investigating the northern California shore organisms (Hewatt 1935, 1937, 1938, 1940) as they were represented in the Monterey Bay region and felt that it would be desirable to make an intensive study of similar faunas in the Point Conception area. Santa Cruz, the largest of the Santa Barbara Islands, was chosen because its shores have been little disturbed by man. It is privately owned and has not been commercialized in the manner of Santa Catalina, the best known of all of the Channel Islands.

In the summer of 1939, with the aid of Professor G. E. MacGinitie of California Institute of Technology, the writer obtained permission to spend the summer on Santa Cruz to study and collect its little known littoral and sublittoral faunas. The project was financed by the Texas Christian University Science Research Fund. The California Fish and Game Commission very graciously cooperated by furnishing transportation facilities and checking up on our welfare at frequent intervals. To Captain Howard Shebley of "The Bonito," I am indebted for many courtesies. Woodbridge Williams, a senior student at Pomona College, assisted in taking the collections.

Mr. Edwin L. Stanton and Mr. Ambrose Ghereni, owners of Santa Cruz Island, aided in every way possible to make the work successful. In many instances horses were supplied for traveling across the rough terrain, and permission for transportation on their boats was granted at all times.

Specimens collected on the island were sent to many specialists for study and determination. Several new species and one apparently new genus were

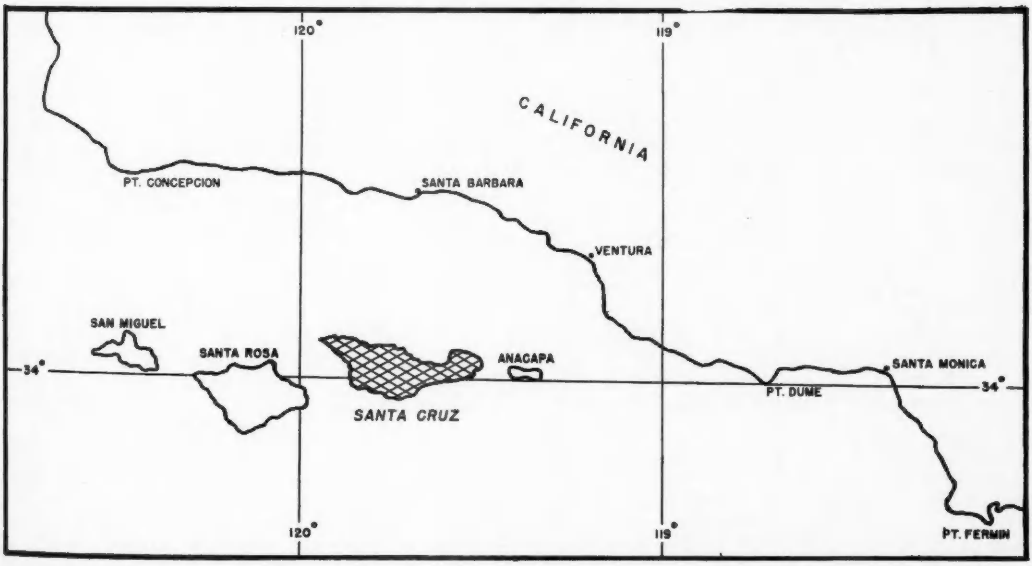

FIG. 1. The Northern Channel Islands of California showing the relative position of Santa Cruz Island.

found in the material, and there were many extensions of ranges. For identifications and information concerning the known ranges of the Santa Cruz Island faunas, the author wishes to acknowledge the receipt of the splendid cooperation of the following persons: Dr. Clarence R. Shoemaker, U. S. National Museum (amphipods); Drs. E. and C. Berkeley, Pacific Biological Station (annelids); Dr. Raymond C. Osburn, Ohio State University (bryozoa); Dr. S. S. Berry, Redlands, California (chitons); Mr. Steve A. Glassell, Beverly Hills, California (brachyurans); Dr. A. Myra Keen, Stanford Museum of Paleontology (gastropods and pelecypods); Dr. Elisabeth Deichmann, Museum of Comparative Zoology (holothurians); Dr. C. McLain Fraser, University of British Columbia (hydroids); Dr. J. O. Maloney, U. S. National Museum (isopods); Dr. Hubert Lyman Clark, Museum of Comparative Zoology (ophiuroids); Dr. W. A. Hilton, Pomona College (pycnogonids); Dr. Waldo L. Schmitt, U. S. National Museum (shrimps); Dr. Willard G. Van Name, American Museum of Natural History (tunicates).

LOCATION AND GENERAL DESCRIPTION OF THE ISLAND

Santa Cruz Island is located approximately 25 miles directly south of Santa Barbara, California in the latitude 34° N. and longitude 119° 45′, Greenwich meridian. The island is about 25 miles long and varies in width from 2 to 6.5 miles.

The shore line of Santa Cruz Island is extremely irregular and presents a variety of littoral habitats. There are expansive open sandy beaches at each end of the island: Smuggler's Cove at the east end and Christy Beach at the west end. Protected and exposed rocky beaches are represented at numerous points. Most of the rocky shore line of the island is vertical and inaccessible except at the mouths of streams.

Geology

The geological features of the island are described by Bremner (1932). A metamorphosed series of rocks, possibly of Jurassic Age, are the oldest rocks on the island. Tertiary sediments and Tertiary volcanic extrusives form a large percentage of the exposed rocks. A series of marine terraces give evidence of the intermittent uplifting of the island mass during Quarternary time.

From about the middle of the island to the eastern end there is a "main mountain ridge." From the center of the island to the westward there are two mountain ridges separated by a canyon. The greatest height of the island is reached on the western end of the northern range where Mount Diablo rises slightly above 2,400 feet. The slopes of the mountain ranges toward the central valley are very steep and covered with a thick growth of shrubs and trees. The slopes toward the northern and southern shores are highly dissected by intermittent streams which make traveling parallel to the shore extremely difficult.

Temperatures of the Water and Air

The temperatures of the surface water below Point Conception are higher than those north of that region during corresponding seasons. In 1932 the temperatures of the surface water in Monterey Bay (Hewatt, 1937, p. 167) during the summer months ranged between 11.7° and 14.5° C. While the present work was in progress on Santa Cruz Island the water temperatures varied from 14.5° to 18.5° C. The temperatures were taken at several stations on the island and are recorded in Table 1.

TABLE 1. Temperature and atmosphere records on Santa Cruz Island, California.

Station	Date	Time	Air temp.	Water temp.	Overhead
Scorpion Hbr....	6-20-39	2:00 p.m.	18.5	16	foggy
Scorpion Hbr....	6-21-39	2:30 p.m.	17.0	14.5	cloudy
Scorpion Hbr....	6-23-39	4:30 p.m.	16.0	14.5	cloudy
Scorpion Hbr....	6-26-39	2:30 p.m.	18.0	15.5	clear
Scorpion Hbr....	6-27-39	3:00 p.m.	18.0	16.0	clear
Scorpion Hbr....	6-28-39	3:00 p.m.	16.0	15.5	foggy
Scorpion Hbr....	6-29-39	12:30 N.	19.0	16.5	clear
Scorpion Hbr....	6-30-39	12:00 N.	18.0	16.0	clear
Scorpion Hbr....	7- 1-39	12:00 N.	18.0	16.0	clear
Scorpion Hbr....	7- 3-39	1:00 p.m.	20.0	17.0	clear
Scorpion Hbr....	7- 3-39	6:30 p.m.	15.5	15.5	foggy
Scorpion Hbr....	7- 5-39	11:00 a.m.	16.0	15.0	foggy
Pelican Bay.....	7- 7-39	3:00 p.m.	16.5	16.0	foggy
Pelican Bay.....	7-14-39	3:00 p.m.	16.5	15.5	foggy
Pelican Bay.....	7-15-39	12:00 N.	20.5	17.5	clear
Pelican Bay.....	7-15-39	5:00 p.m.	16.0	17.0	foggy
Pelican Bay.....	7-17-39	1:00 p.m.	18.0	17.0	clear
Christy Beach...	7-19-39	1:00 p.m.	17.5	16.5	clear
Christy Beach...	7-20-39	9:00 a.m.	16.5	16.5	foggy
Pelican Bay.....	7-21-39	12:00 N.	20.0	18.0	clear
Pelican Bay.....	7-26-39	4:00 p.m.	16.5	18.5	foggy
Willow Hbr......	7-31-39	3:00 p.m.	18.0	18.0	clear
Willow Hbr......	8- 2-39	1:00 p.m.	18.0	18.0	clear

The temperature records taken by the *E. W. Scripps* on Cruises III and IV during the summer of 1938 show the variations of the surface water temperatures over a relatively short period of time. These records were very kindly placed at the author's disposal by Dr. G. F. McEwen of the Scripps Institution of Oceanography, La Jolla, California. In the middle of June the surface temperature around Santa Cruz Island was around 13.5°-14.0° C.; during the middle of August it was between 16.5° and 17.5°.

The air temperature records taken on the island are also shown in Table I.

Currents

The complexity of surface and subsurface currents in the region of the Santa Barbara Islands has been discussed by Tibby (1939), Sperdrup & Allen (1940). Above Point Conception the continental shelf extends only 5 or 6 miles offshore while it extends about 150 miles from the shore along the coast of southern California. This condition probably accounts for the complex nature of the currents in the relatively shallow continental sea around the Channel Islands. The California Current flows in a south-

easterly direction past Point Conception. The California Counter Current originates along the coast of Lower California and flows inshore in a northwesterly direction producing some obvious eddies between the two currents.

The nature of these currents, no doubt, has a profound effect upon the distribution of the littoral faunas of the California coast and their larvae. Scofield (1934) has pointed out the probable effect of these complex currents upon the distribution of sardine larvae. Sverdrup & Allen (1940) have shown the relationship of the currents to the distribution of diatoms of the southern California coast.

TIDES

The tide *reference station* for Santa Cruz Island is the Outer Harbor at Los Angeles. The nature of the tides is similar to that along the remainder of the California coast (Hewatt 1937, pp. 170-172). A period of 25 minutes must be added to the Los Angeles data in calculating the low tide periods for Santa Cruz. During the summer months the best low tide periods occur in the middle of the night which prevents a maximum efficiency in shore collection and observation. The vertical nature of the shore along most of the island coast prevents the exposure of wide areas.

METHODS AND EQUIPMENT

A field laboratory station was first established in an unoccupied fisherman's cabin on the beach at Scorpion Harbor. This laboratory was maintained from June 21 to July 5. From this point it was possible to study the faunas of Scorpion Harbor beach and the adjacent rocky beach to the east of the Harbor. Several trips were made on horseback to Smuggler's Cove.

The equipment consisted mainly of high and low power microscopes, preservatives, anaesthetizing chemicals, small dredge, plankton net, collecting buckets, thermometers, and various sized vials. The mouth of the dredge was made of angle iron and was triangular in shape (about 20 x 20 x 20) with a cutting lip on each side. Three iron rods about 4 feet long extended from the corners of the triangle to a triangular frame at the rear. The net was approximately 12 feet long and about 1 cm. mesh. It was towed behind a skiff propelled by oars. It proved to be very successful for shallow dredging.

A second field laboratory was established at Pelican Bay in one of the several abandoned shacks located on the shore of the bay. The "Prisoner's-Pelican Rockslide" collecting station could be reached from this point. Trips were also made from Pelican Bay to Christy Beach by way of land and water.

On July 28 the laboratory was moved to Willow Harbor on the south side of the island. Here it was maintained until August 27.

DESCRIPTION OF STATIONS WITH FAUNAL LIST

STATION I: SCORPION HARBOR

Scorpion Harbor is located on the northern side of the eastern end of Santa Cruz Island. The shore is marked by many rock slides presenting boulders of varying sizes. An intermittent stream enters the harbor at its west end and forms a rough boulder strewn upper beach which, incidentally, makes the landing of a skiff a hazardous task. At the lowest tide intervals a sandy lower beach is exposed. The shore on each side of the mouth of the stream is marked by inaccessible cliffs of igneous rocks.

There are many outlying "island rocks" along the eastern shore of the harbor which offer splendid collecting areas at low tide. The largest of the "island rocks" is located about four hundred yards east of the stream mouth at Scorpion Harbor. This locality presents, perhaps, the best shore collecting along the entire island. The island rock cannot be reached by following the shore to the east of Scorpion Harbor. One must go about one hundred yards inland and to the east over the extremely rugged terrain in order to reach a deep ravine which leads to the sand bar connecting the rock with the mainland of the island. The shallow water between the rock and the island can be crossed on foot only during relatively low tide periods.

The rocky beach of Scorpion Harbor is protected from strong wave action by a thick growth of float-

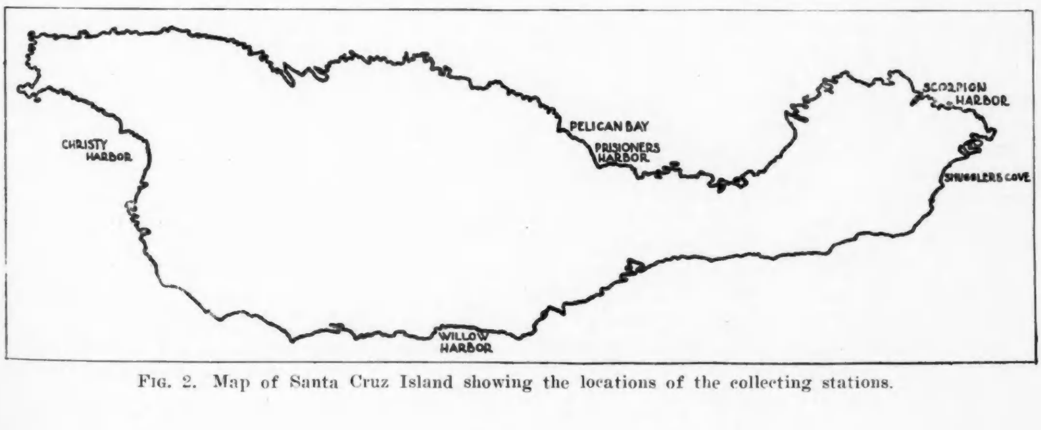

FIG. 2. Map of Santa Cruz Island showing the locations of the collecting stations.

ing kelp which covers the surface of the water approximately 100 feet from the shore. This buffer may account for the relative scarcity of mussels *(Mytilus californianus)* found in the area.

The loose supralittoral boulders offer splendid protection for *Ligyda californica* which is found in great numbers. *Pachygrapsus crassipes* is also numerous in this habitat. When the tide is out these animals move down to lower levels for food.

The uppermost littoral is characterized by the presence of the limpets, *Acmaea scabra* and *A. digitalis,* all of which are small specimens. *A. digitalis* reaches a level in the littoral as high as that of *A. scabra* which was not true in the Monterey Bay area studied (Hewatt 1937, p. 183). These two limpets appear, however, to be adapted to different types of rock surface and are not commonly found closely associated. *A. scabra* is much more common on the rough surfaces. Small specimens of *Littorina planaxis* are abundant on the cliff-like protected shore.

In the mid-levels of the littoral *Balanus glandula* covers the rocks, especially the vertical surfaces. The upper limit of these barnacles is about the 5 foot tide level. The lower limit of *B. glandula* is not sharply marked along the 3 foot level as it was in the protected littoral at Cabrillo Point in Monterey Bay (*ibid.,* p. 182, Fig. 11). The heavy growth of Pelvetia and Fucus which appears to effect the sharp lower limit of the barnacles at Cabrillo Point is not present on the rocks on the east side of Scorpion Harbor. On the west side of the Harbor, however, the thick growth of these plants exists and the line of contact between them and the barnacles is prominent. No explanation can be offered at this time for the peculiar distribution of the algae but it seems certain that *B. glandula* cannot exist beneath the fronds of the algae. Kitching (1935, p. 369) noted a similar limitation of *B. balanoides* on the rock surfaces of the coast of Argyll.

On the east side of the Harbor *B. glandula* extends down to the zero tide level. Among the barnacles are nestled great numbers of *Littorina scutulata.*

Where broad flat surfaces of rock are exposed at mid-tide levels they are commonly covered with *Cribina elegantissima,* the small aggregating green anemone. Among the ever moist bases of the anemones are many specimens of *Epitonium tinctum.* In the Monterey Bay region this niche of the habitat is occupied by *Acanthina spirata* which are relatively rare at Scorpion Harbor. Some of the rocks at these levels are covered with *Aletes squamigerus.*

Among the boulders of the lower middle littoral *Tegula funebralis,* the black turban, is common but not nearly so frequent as it is beneath the layer of Pelvetia and Fucus on the west side of the Harbor. In this part of the littoral the six rayed starfish, *Leptasterias aequalis,* is notably absent. It was not collected anywhere on the island. *Cirolana harfordi* is abundant throughout the intertidal area.

Below the zero tide level are found the many species of hydroids, sponges, and tunicates which characterize this zone of the littoral along the rocky coast of California.

The sandy beach which was exposed only at low tide intervals revealed a great abundance of *Emerita analoga.* From a collection of over 150 specimens no individuals were longer than 11 mm. (carapace length). A search for larger individuals proved fruitless.

In the lists of species given below the relative abundance of each species is indicated by letters: A—abundant; C—common; F—few; R—rare. In a few instances figures are given to indicate the number of specimens collected. It is realized that the method is not entirely satisfactory but in the absence of more quanitative data the plan is followed. Organisms collected from kelp beds in Scorpion Harbor are listed separately.

SCORPION HARBOR

June 23, 24, July 1, 3, 5, 1939 −0.7 tide

Abietinaria amphora	C
Acanthina spirata	R
Acmaea digitalis	A
Acmaea limatula	C
Acamea pelta	C
Acamea scabra	A
Aglaophenia struthionides	F
Aletes squamigerus	C
Alloniscus perconvexus	C
Amaroucium aequali-siphonis	C
Ammothea tuberculata	1
Amphissa versicolor	F
Amphipholis squamata	F
Arabella iricolor	C
Balanus tintinabulum californicus	A
Barleeia subtenuis	R
Betaeus harfordi	C
Calliostoma gloriosum	F
Callitochiton crassicostatus	2
Cancer jordani	F
Cardita ventricosa	C
Caularchus meandricus	A
Chama pellucida	R
Chone infundibuliformis	C
Cirolana harfordi	C
Conus californicus	2
Crago holmesi	2
Crago nigricauda	C
Crangon clamator (ovig.)	C
Crepidula numeria	F
Crepidula sp.	1
Cribrina elegantissima	A
Cribrina xanthogrammica	R
Crisia pacifica	C
Cucumaria lubrica	C
Cyanoplax hartwegii	1
Demonax leucaspis	C
Diaulula sandiegensis	C
Diodora murina	C
Elasmopus sp.	2
Elasmopus antennatus	1
Emerita analoga	A
Epiactis prolifera	F
Epitonium tinctum	A
Euherdmania claviformis	A
Eupentacta quinquesemita	C

Eurystheus tenuicornis	1
Eurythoe paupera	C
Exosphaeroma amplicauda	C
Fissurella volcano	A
Fusinus luteopictus	C
Halosydna insignis	C
Haliotis cracherodii	C
Hapalogaster cavicauda	C
Harmathoe hirsuta	1
Hemipodia borealis	5
Hermissenda crassicornis	C
Homalopoma bacula	C
Hyale frequens	1
Ischnochiton (Lepidozona) californiensis	4
Isociona lithophoenix	C
Lacuna unifasciata	C
Lagenipora erecta	R
Lepidochitona lineata	A
Leuconia heathi	A
Ligyda occidentalis	C
Lissodendoryx noxiosa	R
Lophopanopeus heathi	C
Lophopanopeus leucomanus	C
Lottia gigantea	F
Lumbrinereis erecta	2
Marginella californica	R
Megatebennus bimaculatus	C
Megathura crenulata	C
Melita palmata	1
Mitella polymerus	F
Mitrella carinata	F
Mitra idae	C
Mopalia muscosa	C
Mopalia aff. *ciliata*	v
Mytilimeria nuttallii	C
Mytilus californianus—small	R
Nainereis laevigata	4
Nassarius mendicus	C
Nereis dumerilii var. *agassizi*	C
Nereis callaona	2
Nereis neonigripes	6
Nereis pelagica	6
Norrisia norrisii	R
Odontosyllis parva	1
Oncoscolex pacificus	1
Ophiactis simplex	C
Ophiothrix spiculata	C
Pachycheles rudis	C
Pachygrapsus crassipes	A
Pagurus hirsutiusculus (ovig.)	A
Pagurus samuelis	C
Paracerceis cordata (on coralline algae)	A
Paraxanthias taylori	C
Parorchestes sp.	C
Patiria miniata	F
Pentidotea aculeata	C
Petrolisthes rathbunae (ovig.)	18
Physcosoma agassizii	A
Pisaster giganteus	C
Planocera californica (?)	A
Pleustes depressus	1
Polyophthalmus pictus	R
Pontogeneia sp.	2
Porcellio laevis	C
Pseudopotamilla occeolata	R
Psolas chitinoides	C
Pugettia richii	C
Purpura nuttallii	C
Pycnogonum rickettii	1
Rhabdodermella nuttingi	A
Rostanga pulchra	C
Sabellaria californica	C
Saxicava arctica	A
Sertularella turgida	C
Septifer bifurcatus	A
Smittina trispinosa	C
Spirobranchus spinosus	C
Spirontocaris palpator	1
Strongylocentrotus purpuratus	C
Strongylocentrotus franciscanus	R
Stichopus californicus	C
Styela (Katatropa) vancouverensis	R
Syllis elongata	2
Syllis hyalina	2
Tegula brunnea	R
Tegula funebralis	C
Tethys californica	R
Thais emarginata	R
Thormora johnstoni	2
Thyonepsolus nutriens	R
Trypanosyllis gemmipara	2
Volsella modiolus	C

SCORPION HARBOR

Outlying Island Rocks to East

June 25-July 4, 1939 −.4 tide

Acanthina spirata	C
Acmaea digitalis	A
Acmaea limatula	A
Acmaea pelta	C
Acmaea scabra	A
Acteocina culcitella	R
Ammothea tuberculata	2
Amphissa versicolor	C
Barleeia subtenuis	C
Bittium attenuatum multifilosum	R
Callianassa affinis	3
Cancer jordani	C
Chama pellucida	C
Clavelina huntsmani	C
Clotenia occidentalis	1
Conus californicus	C
Cribrilina hippocrepis	C
Crisia pacifica	C
Dendrobeania laxa	C
Distaplia occidentalis	C
Epiactis prolifera	C
Epitonium insculptum	R
Eudendrium carneum	R
Eudistoma psammion	C
Euherdmania claviformis	C
Fissurella volcano	C
Fusinus cf. *kobelti*	R
Haliotis fulgens	R
Haminoea vesicula	2
Hapalogaster cavicauda	1
Hippolyte californiensis (ovig.)	1
Homalopoma bacula	C
Lecythorhynchus marginatus	1
Lumbrienereis erecta	2
Mitella polymerus	F
Mitra idae	C
"Murex" gemma	C
Mytilus californianus	F
Nereis procera	1
Norrisia norrisii	C

Olivella baetica	R
Olivella biplicata	A
Ophioderma panamensis	C
Pagurus hirsutiusculus	A
Pagurus samuelis	A
Paraxanthias taylori	C
Phoxichilidium compactum	1
Pseudopotamilla occelolata	C
Pugettia dalli	C
Pugettia richii	C
Purpura nuttallii	2
Rhabdodermella nuttingi	C
Seila montereyensis	R
Sertularella turgida	C
Sertularia cornicina	A
Spirontocaris carinata	2
Spirontocaris picta	2
Styela gibsii	C
Styela vancouverensis	R
Tanystylum californicum	1
Thais emarginata	C
Tricellaria occidentalis var. *catalinensis*	A
Tritonalia foveolata	1
Volsella modiolus	C

SCORPION HARBOR KELP BEDS

June 25, 1939

Amphithoe humeralis	1
Amphithoe scitula	3
Amphithoe sp.	15
Aoroides californica	4
Crepidula sp.	1
Ericthonius brasiliensis	1
Eucopella everta	C
Hyale frequens	5
Lacuna porrecta	C
Lacuna unifasciata	C
Mitrella carinata	C
Mitrella gausapata	C
Obelia commissuralis	A
Obelia dichotoma	C
Paracerceis cordata	A
Plumularia lagenifera	C
Plumularia paucinema	R
Pontogenia sp.	1
Sertularella turgida	C
Unidentified nudibranchs	C

STATION II: SMUGGLER'S COVE

Smuggler's Cove is located at the east end of Santa Cruz Island and can be reached safely only by land. It lies at the mouth of an intermittent stream which is dry throughout the summer months. There is an extensive sandy beach, about three fourths of a mile long. At each end of the sandy beach the shore is rocky. The heavy surf along the beach makes the Cove a dangerous landing place for a skiff.

From our base at Scorpion Harbor we traveled the two miles distance over the extremely rugged terrain on slow sure-footed horses. All of our collecting equipment was carried in burlap bags. The trip to Smuggler's Cove took over an hour each way. The "collecting tides" occurred soon after midnight and it was necessary to make the trip in the middle of the night and to use kerosene lanterns and flashlights in collecting before dawn at the lowest tide levels.

Along the southern end of the beach at Smuggler's Cove the boulders at mid-tide levels which are protected from heavy surf are covered with a thick growth of Pelvetia and relatively few fronds of Fucus. The lower rocks are covered with many species of red algae. Vast beds of Zostera cover the lowest intertidal region.

The fauna of the higher intertidal rocks is similar to those of Scorpion Harbor.

In the middle tide levels *Acanthina spirata* is common among the rock barnacles. The Pelvetia beds mark the lower limit of Balanus. Tegula is the most abundant snail among the Pelvetia fronds. Three species and one subspecies of Tegula were collected from the rocks at Smuggler's Cove. In a random collection of 25 specimens *T. funebralis* and *T. gallina tincta* were about equally represented. Five of the shells were *T. gallina* and one was *T. aureotincta.* No differences in the habitats of these species were observed; in fact, with the exception of *T. aureotincta* it was not possible to make definite determinations of the species in the field. More careful collecting in the area might reveal more limited distribution among these species. It would be interesting to know if these forms are found together in any other region along the Pacific coast.

SMUGGLER'S COVE

June 24 and July 2, 1939 -.7 tide

Acanthina spirata	C
Acmaea digitalis	C
Acmaea limatula	A
Acmaea paleacea	R
Acmaea pelta	F
Acmaea scabra	A
Acmaea scutum	A
Aglaophenia struthionides	C
Aletes squamigerus	C
Allorchestes sp.	5
Amaroucium aequali-siphonis	F
Ammothea tuberculata	1
Amphipholis squamata	C
Amphissa versicolor	A
Amphithoe ramondi	2
Amphithoe simulans	8
Anachis lineolata	2
Audouinia tentaculata	1
Barentsia gracilis	C
Barleeia haliotiphila	3
Calliostoma supragranosum	R
Cancer jordani	C
Caulibugula occidentalis	R
Chama pellucida	C
Cerithiopsis pedroana	2
Cirolana harfordi	A
Clavelina huntsmani	C
Colidotea rostrata (1 ovig.)	2
Conus californicus	R
Cooperella subdiaphana	2
Costazia costazii	C
Crangon clamator	C
Crepidula nummaria	R
Cribrina elegantissima	A
Cribrina xanthogrammica	C
Crisia pacifica	R

Cucumaria lubrica	C
Cyanoplax hartwegii	C
Diaulula sandiegensis	C
Distaplia occidentalis	C
Emerita analoga	A
Epitoneum tinctum	C
Esperiopsis originalis	C
Eucopella everta	A
Eucratea chelata	R
Eudistoma psammion	C
Euherdmania claviformis	C
Eupentacta quinquesemita	2
Fissurella volcano	A
Gadinia reticulata	C
Glans carpenteri	C
Haliotis rufescens	A
Halosydna insignis	C
Hermissenda sp.	C
Hippolysmata californica (1 ovig.)	C
Homalopoma bacula	2
Holoporella aperta	A
Hyale frequens	2
Hyale perieri	3
Idothea rectilinea	3
Ischnochiton (Lepidozona) californiensis	1
Kellia laperousii	C
Lacuna unifasciata	2
Lepidochitona dentiens	5
Leucosolenia eleanor	C
Ligyda occidentalis	A
Littorina planaxis	C
Littorina scutulata	A
Lophopanopeus heathi	R
Lottia gigantea	C
Lumbrinereis erecta	2
Lumbrinereis latreilli	3
Lyonsia (Entodesma) inflata	1
Megatebennus bimaculatus	R
Mesenteripora meandrina	C
Milneria kelseyi	1
Mitella polymerus	R
Mitrella carinata	C
Mitrella gausapata	F
Mitromorpha filosa	F
Mopalia muscosa	C
Mytilus californianus	C
Mytilus stearnsii	R
Nainereis laevigata	4
Nereis pelagica	C
Nuttallina c.f. *californica*	6
Odontosyllis phosphorea	1
Odostomia (Chrysallida) virginalis	R
Odostomia (Evalea) angularis	R
Ophiactis simplex	5
Ophioplocus esmarki	C
Ophiopteris papillosa	1
Ophiothrix spiculata	7
Ophlitospongia pennata californiana	C
Pachycheles rudis	C
Pachygrapsus crassipes	A
Pagurus samuelis	A
Paracerceis cordata	C
Patiria miniata	F
Petrolisthes cinctipes	R
Phasianella pulloides	C
Physcosoma agassizii	C
Polypus bimaculatus	1
Polyophthalmus pictus	3
Pontharpinia obtusidens	1
Porcellio laevis	C
Pseudomelatoma sp.	1
Pugettia dalli	C
Purpura nuttalii	F
Rhabdodermella nuttingi	A
Rostanga pulchra	C
Sabellaria californica	C
Salmacina dysteri var. *tribranchiata*	C
Saxicava arctica	A
Scrupocellaria californica	C
Seila montereyensis	2
Spirontocaris picta (2 ovig.)	C
Strongylocentrotus purpuratus	C
Tegula aureotincta	R
Tegula gallina	F
Tegula gallina tincta	C
Tegula funebralis	C
Thais emarginata	C
Transennella tantilla	3
Tricellaria occidentalis var. *cataliensis*	A
Tritonalia circumtexta	4
Truncatella stimpsoni	2
Turbonilla (Strioturbonilla) aresta	2
Volsella modiolus	C

STATION III: PELICAN BAY

Pelican Bay is a relatively small cove located about the middle of the north shore of Santa Cruz Island. The land rises abruptly from the water forming an almost vertical wall from 15 to 25 feet high, around the cove. At about mid-tide level there is a rock shelf several feet wide around most of the shore of the bay. At low tide there are many small shallow tide pools formed on the shelf. The surface water of the bay contains a heavy growth of floating kelp.

The rock shelf around the shore is covered with *Mytilus californianus*. The mussels are all relatively small, the larger ones averaging only about 3 inches in length. A very abundant fauna exists among and beneath the mussels. The inhabitants of the mussel beds only are listed below.

Immediately to the west of the landing dock at Pelican Bay there is an overhanging ledge of rock, beneath which a shallow cave has been formed. The damp walls of the cave are covered with a thick growth of encrusting algae and appears to present an optimum habitat for *Littorina planaxis*. The snails are very numerous and are much larger than any others which the writer has collected along the California coast.

At the mouth of a canyon located about one-half mile west of Pelican Bay there is a cave in the vertical rock wall. The inclosure is about twenty feet long and ten feet wide. It has been formed by a fault in the volcanic rocks. Water remains in the cave at a depth of about two feet even at low tide intervals. Very few organisms were found in the dark cave but they are listed below since some of them were not found elsewhere on the island.

PELICAN BAY

July 18-25, 1939 Low tide

Aega leconti	R
Allorchestes sp.	8

Ammothea tuberculata	3
Amphipholis squamata	1
Amphissa versicolor	A
Amphithoe humeralis	1
Antennella avalonia	C
Arabella iricolor	4
Arabella semimaculata	C
Balanus glandula	C
Balanus tintinabulum californicus	A
Bittium interfossum	1
Bugula neritina	A
Calliostoma supragranosum	C
Caprella acutifrons	1
Caprella acutifrons var. *verrucosa*	5
Celleria diffusa	C
Chaetopleura (Pallochiton) gemma	1
Chaetopleura (Pallochiton) sp.	1
Chama pellucida	C
Cirolana harfordi	A
Clianella elegans	C
Crisia pacifica	C
Dynamene dilatata	1
Dynamemella glabra	1
Elasmopus antennatus	1
Eucopella everta	C
Eudendrium californicum	C
Eupentacta quinquesemita	C
Fabia subquadrata	C
Gians carpenteri	C
Halosydna Johnsoni	6
Halosydna insignis	12
Hippothoa hyalina	C
Ischnochiton (Lepidozona) sp.	1
Irus lamellifer	1
Lecythorhynchus marginatus	7
Leuconia heathi	A
Lithophaga plumula	C
Lophopanopeus heathi	C
Membranipora tuberculata	A
Mitella polymerus	A
Mopalia aff. *ciliata*	1
Mopalia muscosa	3
Mytilus californianus (small)	A
Nereis callaona	2
Nereis neonigripes	6
Nereis pelagica	C
Nereis pseudoneanthes	2
Nuttallina californica	C
Ophiactis simplex	C
Ophiothrix spiculata	C
Pachycheles rudis	C
Pachygrapsus crassipes	A
Parastichopus parvimensis	R
Paraxanthias taylori	C
Pentidotea aculeata	1
Petricola carditoides	C
Petrolisthes cinctipes (3 ovig.)	5
Petrolisthes n. sp. (1)	2
Phasianella pulloides	C
Philobrya setosa	C
Pinnotheres concharum	C
Platynereis dummerilii var. *agassizi*	C
Plumularia lagenifera	C
Pugettia producta	R
Pugettia richii (ovig.)	C
Purpura nuttallii	C
Pycnogonum sternsi	1
Saxicava arctica	A
Scyra acutifrons	C
Semile rupicola	C
Sertularella turgida	
Sertularia cornicina	
Sertularia erecta	
Sertularia furcata	
Syllis armillaris	1
Synthecium cylindricum	C
Tegula funebralis	A
Thais emarginata	A
Thalamoporella gothica var. *prominens*	A
Tricellaria occidentalis var. *cataliensis*	A
Tritonalia circumtexta	C
Volsella capax	A

Cave one-half mile west of Pelican Bay

July 7, 1939

Chromodoris macfarlandi	1
Gadinia reticulata	C
Linkia columbiae	2
Nassarius mendicus cooperi	2
Ophiothrix spiculata	4

Station IV: Prisoner's-Pelican Rockslide

The shore line between Pelican Bay and Prisoner's Harbor is extremely dissected and is inaccessible by land along most of the route. Almost midway between the two harbors there is an extensive rockslide which can be reached only with great difficulty from Pelican Bay. The slide affords one of the best open beach intertidal collecting regions on the island.

The most characteristic feature of the rockslide habitat is the presence of low-level tidepools the bottoms of which are covered with large purple sea urchins, *Strongylocentrotus purpuratus.* The tidepools also contained numerous specimens of the giant green anemone, *Cribrina xanthogrammica.* The webbed starfish, *Patiria miniata* was found only occasionally in the tidepools and *Pisaster ochraceus* was fairly common. One specimen of *Haliotis corrugata,* the only one collected on the island, was found at this locality. *H. fulgens,* mostly young specimens, were common.

Prisoner's-Pelican Rockslide

July 16 and 17, 1939 Tide –1.5

Acanthina spirata	C
Acmaea digitalis	F
Acmaea insessa	C
Acmaea limatula	A
Acmaea mitra	A
Acmaea scabra	A
Acmaea scutum	A
Aletes squamigerus	A
Amphipholis squamata	A
Amphissa versicolor	A
Amphithoe ramondi	1
Ascidia californica	R
Astrometis sertulifera	C
Balanus glandula	A
Balanus tintinabulum californicus	C
Barleeia subtenuis	A
Betaeus harfordi (ovig.)	C
Calliostoma costatum	R
Caprella acutifrons var. *verrucosa*	R
Caprella brevirostris	R

Cerithiopsis diegensis	R
Chama pellucida	C
Cirolana harfordi	A
Cirriformia (Audouinia) luxuriosa	C
Conus californicus	F
Crangon clamator (2 ovig.)	5
Cribrina elegantissima	A
Cribrina xanthogrammica	C
Cycloxanthops novemdentatus	2
Dynamenella glabra	C
Elasmopus sp.	R
Epitonium tinctum	R
Ericthonius brasiliensis	4
Eudistoma diaphanes	4
Eupentacta quinquesemita	R
Euphrosyne hortensis	C
Eurystheus tenuicornis	1
Fissurella volcano	C
Fusinus luteopictus	C
Geodia mesotriaena	C
Glans carpenteri	C
Haliotis corrugata	1
Haliotis fulgens	C
Halosydna johnsoni	C
Halosydna insignis	C
Hapalogaster cavicauda	F
Harmathoe imbricata	1
Henricia leviuscula	F
Homalopoma bacula	A
Homalopoma supranodosum	C
Hyale frequens	C
Irus lamellifer	R
Ischnochiton (Lepidozona) californiensis	5
Ischnochiton (Lepidozona) c.f. *sinudentatus*	3
Lacuna porrecta	C
Ligyda occidentalis	C
Liotia fenestrata	C
Littorina planaxis	C
Littorina scutulata	A
Lophopanopeus heathi	C
Lophopanopeus leucomanus	4
Lottia gigantea	C
Maera simile	2
Marginella californica	R
Megatebennus bimaculatus	F
Megathura crenulata	F
Microporella californica	C
Mitella polymerus	F
Mitra idea	C
Mitrella carinata	C
Mitrella gausapata	C
Mopalia aff. *ciliata*	1
Mytilus californianus	F
Nainereis laevigata	F
Nereis neonigripes	6
Nereis pelagica	C
Nereis vexillosa	2
Norrissia norrisii	C
Ophiactis simplex	C
Ophioplocus esmarki	C
Ophiothrix spiculata	C
Pachycheles rudis	F
Pachygrapsus crassipes	A
Pagurus hirsutiusculus	A
Pagurus samuelis	C
Paracerceis cordata	A
Paraxanthias taylori	C
Patiria miniata	F
Pentidotea aculeata	C
Periclimenes tenuipes (ovig.)	2
Petrolisthes rathbunae	3
Petrolisthes n. sp. (2)	8
Physcosoma agassizii	C
Pisaster ochraceus	C
Planocera californica	A
Pontogeneia sp.	2
Pugettia dalli	C
Pugettia producta	F
Pugettia richii	C
Purpura nuttallii	F
Scyra acutifrons	1
Seila montereyensis	R
Septifer bifurcatus	C
Spirontocaris palpator	5
Spirontocaris picta	5
Strongylocentrotus franciscanus	A
Tegula funebralis	C
Tegula galena	A
Tetraclita squamosa rubescens	A
Thais emarginata	C
Thalamoporella gothica var. *prominens*	A
Thelepus setosus	C
Tonicella liniata	1
Tricellaria occidentalis var. *catalinensis*	R
Triopha carpenteri	C
Tritonalia circumtexta	R
Tritonalia gracillima	R
Tritonalia interfossa	C
Volsella modiolus	A

STATION V: CHRISTY BEACH

Along the middle of the western shore of Santa Cruz Island is an extensive sandy beach, Christy Beach. It is about one mile in length and is continuously beaten by a heavy surf. At the south end of the beach are rocky cliffs and a boulder-strewn beach. The fauna of Christy Beach was not carefully collected and recorded since it was accessible only by land from our bases at Pelican Bay and Willow Harbor. About a half day was spent in the area.

The list of organisms recorded for the beach are included since some of them were not found along other parts of the coast line visited and because of the abundance and size of some of the specimens. Among the boulders at the south end of Christy Beach the writer stood on one spot and counted 97 black abalones, *Haliotis cracherodii.* In some places they were so numerous that as many as five and six specimens were stacked one on the other. The author has never seen any similar concentration of this abalone along the California coast. Abalones are commonly used for bait by lobster fishermen in this region. The inaccessibility of Christy Beach from the water, because of the violent surf action, may account for the abundance of the abalone in this region.

A very large specimen of *Lepidopa myops* was collected on the sandy beach. Mr. Steve A. Glassell, who identified the brachyurans of the collections, stated that it is the largest specimen of that species which he has seen. The length was 18 mm. and the

width, including the spines, was 22.5 mm. Only one small live specimen of *Tivela stultorum* was collected but there were many shells along the beach.

CHRISTY BEACH

July 19, 1939

Acanthina spirata	C
Alloniscus perconvexus	C
Amaroucium aequali—siphonis	A
Amphithoe simulans	1
Callianassa affinis	2
Caprella acutifrons	R
Chama pellucida	C
Cyanoplax hartwegii	3
Dendrochiton sp.	1
Distaplia occidentalis	1
Haliotis cracherodii	A
Lepidopa myops	C
Lophopanopeus heathi	C
Lottia gigantea	A
Marginella regularis	C
Nasarius fossatus	C
Nuttallina californica	C
Odontosyllis polycera	1
Orchestoidea californiana	A
Pagurus hirsutiusculus	C
Polypus bimaculatus	1
Photis californica	1
Syllis fasciata	1
Tivela stultorum	1
Tritonalia circumtexta	C
Tylos punctatus	C

STATION VI: WILLOW HARBOR

The southern shore of Santa Cruz Island is marked by a series of alternating canyons and ridges which extend, almost perpendicular to the shore line, inland to the main southern longitudinal ridge of the island. The ridges end abruptly in steep inclines along the shore. A relatively permanent fresh water stream is found in each of the larger canyons.

Willow Harbor is located at the mouth of one of the canyons near the middle of the southern shore of the island. A permanent stream empties into the harbor. The best collecting area in the region of Willow Harbor is along the beach which extends for about one hundred yards east of the harbor. A rocky shelf which is exposed only during low tide periods is present on this part of the shore. There are many large tidepools along this part of the beach formed by intermittent dykes which run parallel to the shore. There is also a small island in the harbor which affords good collecting at low tide periods.

WILLOW HARBOR

July 30, 1939 –.4 tide

Abietinaria amphora	C
Aglaophenia struthionides	C
Alcyonidium polyoum	C
Allorchestes sp.	2
Amphipholis squamata	C
Amphissa undata	C
Amphissa versicolor	A
Amphithoe scitula	2
Amphithoe simulans	4
Anachis lineolata	1
Anomia peruviana	C
Calliostoma supragranosum	R
Callistochiton crassicostatus	1
Campanularia denticulata	A
Cancer jordani (2 ovig.)	C
Caprella acutifrons	C
Caprella acutifrons var. *verrucosa*	C
Caprella aequilibra	C
Cellaria mandibulata	A
Chlamys hastatus	C
Cirolana harfordi	C
Conus californicus	A
Crangon clamator	3
Crisia pacifica	C
Cucumaria lubrica	R
Cycloxanthops novemdentatus	R
Cypraea spadicea	C
Diaperoecia palmata	C
Didemnum carnulentum	C
Distaplia occidentalis	C
Elasmopus sp.	3
Epitonium crenimarginatum	R
Epitonium tinctum	A
Euherdmania claviformis	C
Eunice enteles	3
Eupentacta quinquesemita	C
Eurocyde spinosa	1
Fusinus luteopictus	C
Geodia mesotriaena	C
Glans carpenteri	C
Halosydna johnsoni	C
Hemigrapsus sp.	1
Hemipodia borealis	2
Hipponix cranioides	2
Hipponix tumens	4
Holoporella aperta	C
Homalopoma carpenteri	A
Hyale frequens	5
Ischnochiton (Stenoplax) sp.	1
Ischnochiton (Lepidozona) sp.	1
Lacuna porrecta	1
Lacuna unifasciata	2
Lecythorhynchus marginatus	3
Leucetta losangelensis	C
Lithophaga plumula	C
Littorina planaxis	C
Littorina scutulata	A
Lophopanopeus heathi	C
Megatebennus bimaculatus	C
Melita palmata	4
Membranipora tuberculata	A
Microporella californica	C
Mitrella carinata	C
Mitrella gausapata	1
Murex petri	C
Nainereis laevigata	C
Neopleustes sp.	2
Nereis pelagica	A
Nereis pseudoneanthes	2
Norrisia norrisii	C
Nuttallina californica	C
Ophiactis simplex	C
Ophionereis eurybrachiplax	R
Ophiothrix spiculata	C
Paracerceis cordata	C
Paragrubia uncinata	2
Paraxanthias taylori	C

Pentacta trachyplaca	1
Pentidotea aculeata	C
Philobrya setosa	C
Phyllodoce madeirensis	C
Physcasoma agassizii	A
Platynereis dumerilli agassizi	C
Plumularia alicia	C
Plumularia lagenifera	A
Podocerus spongicolus	3
Polyclinum planum	
Pseudochama exogyra	
Pseudopotamilla occelata	
Psolus chitinoides	C
Pugettia producta	C
Pugettia richii	C
Purpura nuttallii	
Sabellaria californica	
Saxicava arctica	C
Schistocomus hiltoni	
Schizoporella insculpta	A
Scyra acutifrons	C
Serpula vermicularis	
Sertularella turgida	
Smittina collifera	
Spirobranchus spinosus	
Spirontocaris palpator (ovig.)	1
Syllis elongata	
Syllis fasciata	
Tanystylum californicum	1
Tanystylum intermedium	1
Tethys californica	C
Thormora johnstoni	
Thyone rubra	C
Thyonepsolus nutriens	C
Tricellaria occidentalis var. *catalinensis*	
Trypanosyllis gemmipara	

PHYLOGENETIC LIST OF INTERTIDAL SPECIES

A complete list of identified intertidal species is given below. Where it was possible to obtain the information from specialists on the different groups or from available literature the known ranges of the species are indicated after the names. The excellent paper by Myra Keen (1937) on the Mollusca gives valuable and detailed information on the known ranges of the members of that group. The latitudes of their northern and southern limits are given along with an indication of the mid-point of the ranges. Similar information on other large groups would be of value in distribution studies.

Since the exact limits of the ranges of all of the Santa Cruz Island species are not available at the present time a somewhat arbitrary method is used for indicating the distribution of the species. It appears to be the most common method used by taxonomists for designating the distribution of a species.

An explanation of the abbreviations given after the species names is as follows:

Cal.—limited to the California coast both north and south of Point Conception.

S. Cal.—limited to the California coast south of Point Conception.

Cos.—having a wide distribution; reported from both Atlantic and Pacific coasts.

N.S.—ranging both north and south of the California coast.

N.—reported north of California but not reported south of that state.

S.—species which are found south of California but have not been reported north of the state.

(N. limit)—not reported from the coast north of the region of Point Conception.

(S. limit)—not reported from the coast south of the region of Point Conception.

Porifera
- *Esperiopsis originalis* de Laubenfels—Cal.
- *Geodia mesotriaena* Lendenfeld—N.
- *Isociona lithophoenix* (de Laubenfels)—Cal.
- *Leucetta losangelensis* (de Laubenfels)—S. (N. limit)
- *Leuconia heathi* Urban—Cal.
- *Ophlitaspongia pennata californiana* de Laubenfels—N. (S. limit)
- *Rhabdodermella nuttingi* Urban—Cal.

Hydrozoa
- *Abietinaria amphora* Nutting—N. (S. limit)
- *Aglaophenia diegensis* Torrey—Cal.
- *Aglaophenia inconspicua* Torrey—N.
- *Aglaophenia struthionides* (Murray)—N.
- *Antennella avalonia* Torrey—Cal.
  First time this species has been reported since its discovery in San Francisco Bay (Fraser 1940, p. 41).
- *Bimeria pusilla* Fraser—Cal. (S. limit)
- *Calycella syringa* (Linn.)—N.
- *Eucopella everta* (Clark)—N.
- *Eudendrium californicum* Torrey—N.
- *Eudendrium carneum* Clarke—S. (N. limit)
- *Obelia commissuralis* (McCrady)—S.
- *Obelia dichotoma* (Linn.)—N.
- *Plumularia alicia* Torrey—N.
- *Plumularia lagenifera* Allman—N.
- *Plumularia paucinema* Fraser
  This is a new species described by Fraser (1940, p. 42).
- *Sertularella erecta* Fraser—S. (N. limit)
- *Sertularella turgida* (Trask)—N.
- *Sertularia cornicina* (McCrady)—Cal.
- *Sertularia furcata* Trask—N.
- *Synthecium cylindricum* (Bale)—Cal.

Actinozoa
- *Cribrina elegantissima* (Brandt)—N.
- *Cribrina xanthogrammica* (Brandt)—N.S.
- *Epiactis prolifera* Verrill—N.

Bryozoa
- *Alcyonidium polyoum* (Hassall)—N. (S. limit)
- *Barentsia gracilis* M. Sars—N. (S. limit)
- *Bugula neritina* (Linn.)—S.
- *Caulibugula ciliata* (Robertson)—N.
- *Caulibugula occidentalis* (Robertson)—N. (S. limit)
- *Cellaria diffusa* Robertson—N.
- *Cellaria mandibulata* Hincks—N.
- *Costazia costazii* (Audouin)—S.
- *Crassimarginatella tincta* Hastings—S. (N. limit) (only Galapagos & Mazatlan, Mex.)
- *Cribrilina hippocrepis* Hincks—N.S.
- *Crisia pacifica* Robertson—S. Cal. (N. limit) (San Diego only)
- *Dendrobeania laxa* (Robertson) N. (S. limit)
- *Diaperoecia palmata* (O'Donaghue)—N. (S. limit) (only Br. col.)

Eucratea chelata (Linn.)—N. (S. limit)
Hincksina sp.
Hippothoa hyalina (Linn.)—N.
Holoporella aperta (Hincks)—N.S.
Holoporella hexagonalis Canu and Bassler—S. (N. limit) (Galapagos only)
Idmonea californica D'Orbigny—N.
Lagenipora erecta O'Donaghue—N. (S. limit) (Br. Col. only)
Membranipora membranacea (Linn.)—N. (S. limit)
Membranipora tuberculata (Bosc)—S.
Mesenteripora meandrina (Wood)—N.
Microporella californica (Busk)—N.
Schizoporella insculpta Hincks—N.S.
Scrupocellaria californica Trask—Cal.
Smittina collifera (Robertson)—Cal.
Smittina trispinosa (Johnston)—N.
Thalamoporella gothica var. *prominens* Levinsen—S. (N. limit)
Tricellaria erecta (Robertson)—N. (S. limit)
Tricellaria occidentalis var. *catalinensis* (Robertson) —S. (N. limit)

Amphineura
Callistochiton crassicostatus Pilsbry—N.
Chaetopleura (Pallochiton) gemma ("Carpenter" Dall)
Chaetopleura (Pallochiton) sp.
Cyanoplax hartwegii (Carpenter)—N.
Dendrochiton sp.
Ischnochiton (Lepidozona) californiensis Berry
Ischnochiton (Lepidozona) sinudentatus Carpenter
Ischnochiton (Stenoplax) sp.
Lepidochitona dentiens (Gould)
Mopalia aff. *ciliata* (Sowerby)—N.
Mopalia muscosa (Gould)
Nutallina californica (Nuttall)—N.S.
Tonicella lineata (Wood)—N. (S. limit)

Gastropoda
Acanthina spirata (Blainville)—N.S.
Acmaea digitalis Eschscholtz—N.S.
Acmaea limatula Carpenter—N.S.
Acmaea mitra Eschscholtz—N. (S. limit)
Acmaea paleacea (Gould)—N.S.
Acmaea pelta Eschscholtz—N.S.
Acmaea scabra (Gould)—N.S.
Acteocina culcitella (Gould)—N.S.
Aletes squamigerus Carpenter—N.S.
Amphissa undata Carpenter—S.
Amphissa versicolor Dall—N.S.
Anachis lineolata (Reeve)—S. (N. limit)
Barleeia haliotiphila Carpenter—S.
Barleeia subtenuis Carpenter—S. (N. limit)
Bittium attenuatum multifilosum Bartsch—N.S.
Bittium interfossum Carpenter—S.
Calliostoma costatum (Martyn)—N.
Calliostoma supragranosum Carpenter—S.
Cerithiopsis diegensis Bartsch—S. Cal. (N. limit)
Cerithiopsis perdroana Bartsch—S. (N. limit)
Chromodoris macfarlandi Cockerell
Conus californicus Hinds—S.
Crepidula nummaria Gould—N.S.
Crepidula sp.
Cytharella hexagona (Gabb)—Cal.
Cypraea spadicea Swainson—S.
Diaulula sandiegensis (Cooper)
Diodora murina Dall—S.
Epitonium tinctum (Carpenter)—N.S.
Epitonium insculptum Carpenter—S.
Fissurella volcano Reeve—S.
Fusinus cf. *kobelti* Dall—Cal.
Fusinus luteopictus Dall—S.
Gadina reticulata Sowerby—S.
Haliotis cracherodii Leach—N.S.
Haliotis corrugata Gray—S.
Haliotis fulgens Philippi—S.
Haliotis rufescens Squainson—N.S.
Haminoea vesicula Gould—N.S.
Hermissenda crassicornis Eschscholtz
Hipponix tumens Carpenter
Hipponix cranioides Carpenter—N. (S. limit)
Homalopoma bacula (Carpenter)—N.S.
Homalopoma carpenteri (Pilsbry)—N.S.
Homalopoma supranodosum (Strong)—S. Cal.
Lacuna porrecta Carpenter—N. (S. limit)
Lacuna unifaciata Carpenter—S.
Liotia fenestrata Carpenter—S.
Littorina planaxis Philippi—N.S.
Littorina scutulata Gould—N.S.
Lottia gigantea Sowerby—N.S.
Marginella californica Tomlin—S. (N. limit)
Marginella regularis Carpenter—S.
Megatebennus bimaculatus (Dall)—N.S.
Megathura crenulata Sowerby—S.
Mitra idae Melville—Cal.
Mitrella carinata (Hinds)—S.
Mitrella gausapata (Gould)—N.S.
Moniliopsis filosa (Carpenter)—N.
"*Murex*" *gemma* Sowerby—S. (N. limit)
Murex petri Dall—Cal.
Nassarius fossatus (Gould)—N.S.
Nassarius mendicus Gould—N.S.
Nassarius mendicus cooperi (Forbes)—N.S.
Norrisia norrisii (Sowerby)—N.S.
Odostomia (Chrysallida) virginalis Dall and Bartsch —S. (N. limit)
Odostomia (Evalea) angularis Dall and Bartsch—N. (S. limit)—Ext. of range
Olivella biplicata (Sowerby)—N.S.
Phasianella pulloides Carpenter—S.
Pseudomelatoma sp.
This new species is being described by Dr. Myra Keen, Stanford University.
Purpura nuttallii (Conrad)—S.
Rostanga pulchra MacFarland
Seila montereyensis Bartsch—Cal.
Tegula aureotincta (Forbes)—S.
Tegula funebralis A. Adams—N.S.
Tegula brunnea Philippi—N. (S. limit)
Tegula galena (Forbes)—S.
Tegula galena tincta Hemphill—S.
Tethys californica (Cooper)—S.
Thais emarginata (Deshayes)—N.S.
Triopha carpenteri Stearns
Tritonalia circumtexta (Stearns)—N.S.
Tritonalia foveolata (Hinds)—N.S.
Tritonalia gracillima (Stearns)—Cal.
Tritonalia interfossa (Carpenter)—N.
Truncatella stimpsoni Stearns—S. (N. limit)
Turbonilla (Strioturbonilla) aresta Dall and Bartsch —S. Cal. (N. limit)

Pelecypoda
Anomia peruviana (D'Orbigny)—S.
Chama pellucida Sowerby—N.S.
Chlamys hastatus (Sowerby) N. (S. limit)
Cooperella subdiaphana Carpenter—N.S.
Glans carpenteri (Lamy)—N.

Irus lamellifer (Conrad)—Cal. (North of 33°)
Kellia laperousii (Deshayes)—N.
Lithophaga plumula (Hanley)—S.
Lyonsia (Entodesma) inflata Conrad—S.
Milneria kelseyi Dall—S.
Mytilimeria nuttallii Conrad—N.S.
Mytilus californianus Conrad—N.S.
Mytilus stearnsii Pilsbry and Raymond—S. (N. limit)
Petricola carditoides Conrad—N.S.
Philobrya setosa (Carpenter)—N.S.
Pseudochama exogyra (Conrad)—N.S.
Saxicava arctica (Linn.)—N.S.
Semele rupicola Dall—S.
Septifer bifurcatus (Conrad)—N.S.
Tivella stultorum Mawe—S.
Transennella tantilla (Gould)—N.S.
Volsella modiolus (Linn.)—N.

Cephalopoda
Polypus bimaculatus (Verrill)—S. (N. limit)

Sipunculoidea
Physcasoma agassizii (Keferstein)—N. (S. limit)

Polychaeta
Arabella iricolor (Montagu)—Cos.
Arabella semimaculata (Moore)—Cal.
Chone infundibuliformis Kroyer—N.
Cirriformia (Audoninia) luxuriosa (Moore)—S.
Cirriformia (Audoninia) tentaculata (Montagu)—Cal.
Demonax leucaspis Kinberg—N.S.
Eunice enteles Chamberlin—Cal.
Euphrosyne hortensis Moore—N.
Eurythoe paupera (Grube)—S.
Eurythoe sp.?
Halosydna insignis Baird—N.
Halosydna johnsoni (Darboux)—S.
Harmathoe hirsuta Johnson—S.
Harmathoe imbricata (Linn.)—Cos.
Hemipodia borealis Johnson—N.
Lumbrinereis erecta Moore—Cal.
Lumbrinereis latreilli Audouin and Milne-Edwards—Cos.
Nainereis laevigata (Grube)—Cos.
Nereis callaona (Grube)—Cal.
Nereis neonigripes Hartman—Cal.
Nereis pelagica Linn.—Cos.
Nereis procera Ehlers (?)—N.
Nereis pseudoneanthes Hartman—Cal.
Nereis vexillosa Grube—N.
Odontosyllis parva Berkeley—N. (S. limit)
Odontosyllis phosphorea Moore—Cal.
Odontosyllis polycera (Schmarda)—S. (N. limit)
Oncoscolex pacificus (Moore)—N.
Phyllodoce madeirensis Langerhans—Cos.
Platynereis dumerilli agassizi (Audouin and Milne-Edwards)—N.S.
Polyophthalmus pictus (Dujardin)—Cos.
Pseudopotamilla occelata Moore—N.
Sabellaria californica Fewkes—Cal.
Salmacina dysteri tribranchiata (Moore)—S.
Schistocomus hiltoni Chamberlin—N.
Serpula vermicularis Linn.—Cos.
Spirobranchus spinosus Moore—Cal.
Syllis armillaris Malmgren—Cos.
Syllis elongata (Johnson)—N.
Syllis faciata Malmgren—N.
Syllis hyalina Grube—Cos.
Thelepus setosus (Quatrefages)—Cos.
Thormora johnstoni (Kinberg)—S.
Trypanosyllis gemmipara Johnson—N. (S. limit)

Amphipoda
Allorchestes sp.
Amphithoe ramondi (Audouin)
Amphithoe humeralis Stimpson—N.S.
Amphithoe scitula (Hardord)
Amphithoe simulans Alderman
Amphithoe sp.
Caprella acutifrons Latreille
Caprella acutifrons var. *verrucosa* Boeck
Caprella aequilibra Say
Caprella brevirostris Mayer
Elasmopus antennatus (Stout)
Elasmopus sp.
Eurystheus tenuicornis (Holmes)—N.
Ericthonius brasiliensis (Dana)
Hyale frequens (Stout)
Hyale perieri (Lucas)
Maera simile Stout
Melita palmata (Montagu)
Neopleustes sp.
Orchestia traskiana Stimpson
Paragrubia uncinata (Stout)
Parorchestia sp.
Photis californica Stout
Pleustes depressus Alderman
Pontharpinia obtusidens Alderman
Pontogeneia sp.
Podocerus spongicolus Alderman

Isopoda
Aega leconti (Dana)—N. (Mont. Bay) (S. limit)
Alloniscus perconvexus Dana N. (S. limit)
Cirolana harfordi (Lockington)—N.S.
Clianella elegans Boone
Colidotea rostrata (Benedict)—S. (N. limit)
Dynamene dilatata Richardson—N. (S. limit)
Dynamenella glabra (Richardson)—Cal.
Exosphaeroma amplicauda—N.
Idothea rectilinea Lockington—N.S.
Ligyda occidentalis (Dana)—N.S.
Paracerceis cordata Richardson—N. (S. limit)
Pentidotea aculeata Stafford
Porcellio laevis Latrielle—Cos.
Tylos punctatus Holmes and Gay—S. (N. limit)

Cirripedia
Balanus aquila Pilsbry—Cal.
Balanus glandula Darwin—N.
Balanus tintinabulum californicus Pilsbry—S.
Mitella polymerus (Sowerby)—N.S.
Tetraclita squamosa rubescens Darwin—N.S.

Natantia
Betaeus harfordi (Kingsley)—Cal.
Crago holmesi (Rathbun)—S. (N. limit)
Crago nigricauda (Stimpson)—N.S.
Crangon clamator (Lockington)—N.S.
Hippolysmata californica Stimpson—S. (N. limit)
Hippolyte californiensis Holmes—N.
Periclimenes tenuipes Holmes—S. (N. limit)
Spirontocaris carinata Holmes—Cal.
Spirontocaris palpator (Owen)—N.S.
Spirontocaris picta (Stimpson)—Cal.

Reptantia
Callianassa affinis Holmes—S.
Cancer jordani Rathbun—S.
Cycloxanthops novemdentatus (Lockington)—N.S.
Emerita analoga (Stimpson)—S.

Fabia subquadrata Dana—N.
Hapalogaster cavicauda Stimpson—N.
Hemigrapsus sp.
Lepidopa myops Stimpson—S. (N. limit)
Lophopanopeus heathi Rathbun—Cal.
Lophopanopeus leucomanus (Lockington)—Cal.
Pachygrapsus crassipes—N.S.
Pachycheles rudis (Stimpson)—N. (S. limit with rare except.)
Pagurus hirsutiusculus (Dana)—N.
Pagurus samuelis (Stimpson)—Cal.
Paraxanthias taylori (Stimpson)—S.
Petrolisthes cinctipes (Randall)—N. (S. limit)
Petrolisthes n. sp. (1)
Petrolisthes n. sp. (2)
These two different new species of Petrolisthes are described in a manuscript of Steve A. Glassell.
Petrolisthes rathbunae Schmitt—S. (N. limit)
Pinnotheres concharum (Rathbun)—N.S.
Pugettia dalli Rathbun—S. (N. limit)
Pugettia producta (Randall)—N.S.
Pugettia richii Dana—N.S.
Randallia ornata (Randall)—S.
Scyra acutifrons Dana—N.

Pycnogonida
Ammothea tuberculata Hall—Cal.
Clotenia occidentalis Cole—Cal.
Eurycyde spinosa Hilton—S. (N. limit)
Lecythorhynchus marginatus Cole—S.
Phoxichilidium compactum Hilton—S. Cal. (N. limit)
Pycnogonum rickettii Schmitt—Cal.
Tanystylum californicum Hilton—Cal.
Tanystylum intermedium Cole—Cal.

Asteroidea
Astrometis sertulifera (Xantus)—Cal.
Henricia leviuscula (Stimpson)—N.
Linckia columbiae Gray—S. (N. limit)
Patiria miniata (Brandt)—N.S.
Pisaster giganteus (Stimpson)—N.
Pisaster ochraceus (Brandt)—N.

Echinoidea
Strongylocentrotus franciscanus (A. Agassiz)—N.S.
Strongylocentrotus purpuratus (Stimpson)—N.S.

Holothuroidea
Cucumaria lubrica H. L. Clark—N. (S. limit)
Eupentacta quinquesemita (Selenka)—N. (Rare S. Pt. Concep.)
Parastichopus parvimensis (H. L. Clark)—S. (N. limit)
Pentacta trachyplaca (H. L. Clark)—N. (S. limit)
Psolus chitinoides H. L. Clark—N.
Stichopus johnsoni Theel
Thyone rubra H. L. Clark—N. (S. limit)
Thyonepsolus nutriens H. L. Clark—N. (S. limit)

Ophiuroidea
Amphipholis squamata delle Chiajes—Cos.
Ophiactis simplex (Leconte)—S. (N. limit)
Ophioderma panamensis Lutkin—S. (N. limit)
Ophioplocus esmarki Lyman—N. S.
Ophiopteris papillosa (Lyman)—Cal.
Ophiothrix spiculata Leconte—S.

Tunicata
Amaroucium aequali—siphonis Ritter and Forsyth—Cal.
Ascidia californica Ritter and Forsyth—Cal. (Mainly north)
Clavelina huntsmani Van Name—N. (S. limit)
Didemnum carnulentum Ritter and Forsyth—S. Cal. (N. limit)
Distaplia occidentalis Ritter and Forsyth—N.
Eudistoma diaphanes Ritter and Forsyth—Cal.
Eudistoma psammion Ritter and Forsyth—Cal.
Euherdmania claviformis (Ritter)—Cal.
Polyclinum planum Ritter and Forsyth—Cal.
Styela (Katatropa) vancouverensis (Huntsman)—N. (S. limit)

SHALLOW DREDGINGS

The equipment used and the time available for the dredging operations were entirely inadequate to give anything like a complete picture of the bottom fauna of the shallow water off Santa Cruz Island. There are, however, some interesting records in the material. Relatively shallow water dredging collections were made at ten stations. Five of the stations were located off Scorpion Harbor.

In the lists of animals given below for the dredging stations there are also recorded some figures indicating the numbers of individuals collected. These figures cannot be relied upon to indicate the true relative abundance of the different species since it was not possible under the circumstances to establish a collecting unit of any type. They are simply given for what they may be worth to future collectors in the area.

STATION I: SCORPION HARBOR

June 25, 1939 2-3 fathoms

Aglaophenia digensis	C
Allorchestes sp.	1
Ampharete arctica	2
Amphipholis squamata	C
Amphissa undata	7
Amphithoe humeralis	1
Amphithoe scitula	15
Amphithoe sp.	4
Anoplodactylus erectus	1
Aoroides californica	18
Arctonoe vittata	2
Batea transversa	6
Calliostoma gloriosum	4
Cancer jordani	15
Caprella acutifrons	3
Caprella sp.	
Cellaria mandibulata	C
Chlamys hastatus	8
Clythrocerus decorus	6
Crago nigricauda (ovig.)	2
Ericthonius brasiliensis	2
Eumida sanguinea	1
Eurystheus tenuicornis	25
Hippolyte californiensis (ovig.)	2
Homalopoma carpenteri	3
Hyale frequens	5
Ischyrocerus sp.	27
Lacuna unifasciata	1
Liotia acuticostata	1
Loxorhynchus crispatus	6
Margarites lirulatus	3
Margarites optabolis	2
Melanella micans	3
Mitrella tuberosa	2
Neopleustes sp.	1

Nymphopsis spinosissimus	1
Odontosyllis parva	2
Oenopota grippi	2
Opalia tremperi	2
Palene pacifica	2
Paracerceis cordata	4
Pentidotea resecata	6
Phasianella pulloides	3
Photis californica	3
Platynereis dumerilii var. *agassizi*	2
Pleustes depressus	2
Plumularia lagenfera	C
Podochela hemphilli	4
Pugettia richii	6
Siphodentalium quadrifissatum	1
Spirontocaris palpator (ovig.)	3
Tricellaria erecta	
Tricellaria occidentalis var. *catalinensis*	
Turritella marina	2
Unidentified gastropod	1

Dr. Myra Keen is describing this new genus.

Station II: Scorpion Harbor

June 26, 1939 5 fathoms

Acmaea insessa	2
Aglaophenia struthionides	A
Amphipholis squamata	C
Amphissa versicolor	1
Amphithoe ramondi	1
Amphithoe scitula	6
Amphithoe sp.	1
Aoroides columbiae	5
Barleeia haliotiphila	5
Batea transversa	6
Calliostoma supragranosum	3
Cancer jordani	9
Caprella aequilibra	2
Caprella scaura	1
Cheirimedon sp.	1
Conus californicus	6
Crago holmesi	2
Crago munitella	1
Crepidula excavata	3
Eurystheus tenuicornis	21
Felaniella sericata	1
Gari californica	5
Hinnites multirugosus	6
Ischyrocerus sp.	2
Lacuna unifasciata	4
Leptopecten monotimeris	4
Loxorhynchus crispatus	3
Margarites optabolis	6
Micranellum crebricinctum	9
Mitrella hypodra	11
Mitrella tuberosa	3
Molgula pugetiensis	1
Nassarius cooperi	1
Nemocardium centifilosum	2
Neopleustes sp.	10
Nereis neonigripes	R
"*Nuculana acuta*"	3
Nymphopsis spinosissimus	1
Odostomia c.f. *nemo*	1
Olivella c.f. *baetica*	1
Palene pacifica	2
Pandalus gurneyi	1
Phasianella pulloides	5
Platynereis dumerilii var. *agassizi*	C
Podochela hemphillii	1
Pugettia richii	6
Schizoporella insculpta	A
Spirontocaris cristata (1 ovig.)	3
Spirontocaris lagunae (ovig.)	1
Spirontocaris palpator (9 ovig.)	23
Spirontocaris prionota	1
Sympleustes glaber	2
Tanystylum californicum	1
Thalamoporella gothica var. *prominens*	C
Tricellaria occidentalis var. *catalinensis*	A

Station III: Scorpion Harbor

June 26, 1939 7-10 fathoms

Aglaophenia sp.	
Ampelisca lobata	2
Amphipholis squamata	14
Amphissa undata	1
Amphithoe ramondi	2
Bimeria pusilla	
Calycella syringa	
Cellaria mandibulata	R
Chevalia aviculae	1
Erileptus spinosus	4
Eunice siciliensis	1
Eurystheus tenuicornis	2
Holoporella hexagonalis	C
Idmonea californica	C
Isociona lithophoenix	C
Lima dehiscens	14
Nereis pelagica	6
Ophiothrix spiculata	3
Platynereis dumerilii var. *agassizi*	5
Schizoporella insculpta	A
Scyra acutifrons	1

Station IV: Scorpion Harbor

June 26, 1939 15 fathoms

Ammocheres fusiformis	1
Ampelisca cristata	2
Amphipholis squamata	8
Amphithoe scitula	1
Caprella acutifrons	1
Caprella aequilibra	8
Cucumaria lubrica	1
Erileptus spinosus	8
Gari californica	6
Laonice cirrata	1
Malmgrenia nigralba	1
Ophiopsila californica	1

This is the second known specimen of this ophiuroid which has ever been collected.

Photis californica	1
Platynereis dumerilii var. *agassizi*	5
Schizoporella insculpta	
Semele incongrua	5
Streblosoma bairdi	3
Stylarioides eruca	1

Station V: Scorpion Harbor

June 26, 1939 20 fathoms

Aglaophenia sp.	C
Ampelisca venetiensis	1
Bugula neritina	C
Calliostoma gloriosum	3
Calyptraea contorta	2
Cardita ventricosa	5
Clythrocerus decorus	6

Clythrocerus planus	(2 ovig.)	6
Crago nigricauda		1
Cucumaria lubrica		A
Cytharella hexagona		1
Drilonereis filum		1
Ephesia gracilis		2
Erileptus spinosus		14
Eugyra n. sp.		1
Eurystheus tenuicornis		3
Felaniella sericata		1
Hincksina sp.		
Hipponix tumens		2
Hippothoa hyalina		C
Kellia laperousii		2
Lepidonotus coelorus		6
Lumbrinereis inflata		1
Lyonsia californica		16
Mangelia arteaga roperi		1
Microporella californica		A
Mitromorpha aspera		1
Molgula pugetiensis		1
Molgula regularis		4
Moniliopsis incisa		2
Nemocardium cantifilosum		3
Nereis procera		1
"*Nuculana acuta*"		5
Olivella baetica		2
Ophiothrix spiculata		6
Pagurus sp.		
Pentamera pseudopopulifera		6
Photis californica		A
Phyllodoce madeirensis		4
Pinnotheres concharum		7
Platynereis dumerilii var. *agassizi*		2
Polydora giardi		1
Psammolyce spinosa		2
Spirobranchus spinosus		4
Spirontocaris snyderi	(ovig.)	1
Streblosoma bairdii		1
Styela gibsii		1
Stylarioides inflata		1
Syllis gracilis		1
Thalamoporella californica		R
Trachycardium quadragenarium		2

STATION VI: PRISONER'S HARBOR

July 27, 1939 15-20 fathoms

Light brown mud

Allorchestes sp.		1
Ampelisca macrocephala		1
Amphithoe ramondi		2
Amphithoe scitula		1
Amphithoe simulans		3
Amphiura arcystata		3
Aoroides sp.		1
Bemlos macromerus		1
Bugula neritina		A
Compsomyax subdiaphana		1
Crago holmesi	(ovig.)	2
Crago munitella	(4 ovig.)	5
Crago nigricauda		1
Harmathoe imbricata		1
Hippothoa hyalina		C
Lembos concavus		7
Leptosynapta albicans		A
Lophopanopeus heathi		9
Macoma yoldiformis		2
Microporella californica		A
Mitrella tuberosa		3
Nassarius mendicus var. *cooperi*		4
Nephthys dibranchis		C
Pandalus gurneyi		2
Phasianella pulloides		3
Pinnixia tomentosa		1
Pugettia dalli		2
Schizoporella insculpta		A
Scyra actuifrons		5
Solen sicarius		4
Spirontocaris palpator	(9 ovig.)	15
Thalamoporella gothica var. *prominens*		A
Trachycardium quadragenarium		2
Tricellaria occidentalis var. *catalinensis*		A

STATION VII: PELICAN BAY

July 12 and 18, 1939 5-10 fathoms

Amphithoe ramondi		4
Caprella acutifrons		23
Caprella brevirostris		1
Caprella scaura		2
Hyale frequens		1
Olivella pedroana		1
Platynereis dumerilii var. *agassizi*		2
Spirontocaris palpator	(ovig.)	3

VIII: PELICAN BAY

July 11, 1939 25 fathoms

Rock bottom

Amphithoe sp.		2
Crassimarginatella tincta		C
Ericthonius brasiliensis		3
Halosydna johnsoni		4
Holoporella hexagonalis		A
Melita fresnelii		2
Ophiothrix spiculata		1
Pandalus platyceras		2
Photis californica		1
Platynereis dumerilii var. *agassizi*		3
Spirontocaris cristata	(4 ovig.)	6
Spirontocaris palpator		1
Spirontocaris prionota		2

STATION IX: TINKER'S HARBOR

July 27, 1939 5 fathoms

Nephthys caecoides		1

STATION X: WILLOW-ORQUETO HARBORS

July 30, 1939 7 fathoms

Aglaophenia inconspicua		
Aglaophenia struthionides		
Astraea undosa		C
Balanus aquila		C
Calliostoma gloriosum		R
Cancer jordani		C
Clythrocerus planus		12
Conus californicus		1
Crassimarginatella tincta		C
Crepidula excavata		8
Crisia pacifica		C
Eucopella everta		C
Eurystheus tenuicornis		1
Heterocrypta occidentalis		4
Hippothoa hyalina		C
Idmonea californica		C
Idothea rectilinea		1
Ischyrocerus sp.		3
Kellettia kellettii		2

Leptopecten monotimeris	1
Loxorhynchus crispatus	5
Lyonsia californica	2
Margarites optabilis	5
Microporella californica	C
Mitrella carinata	25
Mitrella gausapata	17
Nassarius mendicus	2
Nassarius mendicus cooperi	1
Nassarius perpinguis	3
Neopleustes sp.	1
Paracerceis cordata	1
Phasianella pulloides	8
Photis californica	1
Randallia ornata	1
Sertularella erecta	A
Solen sicarius	1
Spirontocaris palpator (ovig.)	1
Tanais normani	1
Thalamoporella gothica var. *prominens*	A
Tricellaria occidentalis var. *catalinensis*	A

PHYLOGENETIC LIST OF SUBTIDAL SPECIES

Hydrozoa

Aglaophenia digensis Torrey—Cal.
Aglaophenia inconspicua Torrey—N.
Aglaophenia struthionides (Murray)—N.
Bimeria pusilla Fraser—Cal. (S. limit)
Calycella syringa (Linn.)—N.
Eucopella everta (Clark)—N.
Plumularia lagenifera Allman—N.
Sertularella erecta Fraser—S. (N. limit)

Bryozoa

Cellaria mandibulata Hincks—N.
Crassimarginatella tincta Hastings—S. (N. limit)
Hincksina sp.
Hippothoa hyalina (Linn.)—N.
Holoporella hexagonalis Canu and Bassler—S. (N. limit) (Galapagos only)
Idmonea californica D'Orbigny—N. (S. limit)
Microporella californica (Busk)—N.
Schizoporella insculpta Hincks—N.S.
Thalamoporella gothica var. *prominens* Levinsen—S. (N. limit)
Tricellaria erecta (Robertson)—N. (S. limit)

Gastropoda

Acmaea insessa (Hinds)—N.S.
Amphissa undata Carpenter—S.
Amphissa versicolor Dall—N.S.
Astraea undosa (Wood)—S. (N. limit)
Barleeia haliotiphila Carpenter—S.
Calliostoma gloriosum Dall—Cal.
Calliostoma supragranosum Carpenter—S.
Calyptraea contorta Carpenter—S. (N. limit)
Conus californicus Hinds—S.
Crepidula aculeata (Gmelin)—S. (N. limit)
Crepidula excavata Broderip—S.
Cytharella hexagona (Gabb)—Cal.
Hipponix tumens Carpenter—S.
Homalopoma carpenteri (Pilsbry)—N.S.
Kellettia kellettii (Forbes)—S. (N. limit)
Lacuna unifasciata Carpenter—S.
Liotia acuticostata Carpenter—S.
Mangelia arteaga roperi Dall—S.
Margarites lirulatus (Carpenter)—N.
Margarites optabilis (Carpenter)—S. Cal. (N. limit)
Melanella micans Carpenter)—N.S.
Micranellum cribricinctum (Carpenter)—N.
Mitrella carinata (Hinds)—S.
Mitrella gausapata (Gould)—N.S.
Mitrella hypodra (Dall)—N.S.
Mitrella tuberosa (Carpenter)—N.S.
Mitromorpha aspera Carpenter—N. (S. limit)
Moniliopsis incisa (Carpenter)—N.
Nassarius cooperi (Forbes) N. (S. limit)
Nassarius mendicus Gould—N.S.
Nassarius perpinguis Hinds—N.S.
Odostomia c.f. *nemo* Dall and Bartsch—S. Cal. (N. limit)
Oenopota grippa (Dall)—S. Cal. (N. limit)
Olivella baetica Carpenter—N.S.
Olivella pedroana Conrad—N.S.
Opalia tremperi Bartsch—S. Cal.
Phasianella pulloides Carpenter—Cal.
Siphonodentalium quadrifissatum Pilsbry—S.
Turritella marina Dall—S.
New genus, being described by Dr. Myra Keen, Stanford Museum of Paleontology.

Pelecypoda

Cardita ventricosa Gould—N.
Chlamys hastatus (Sowerby)—Cal. (S. limit)
Chlamys (Leptopecten) monotimeris (Conrad)—N.S.
Compsomyax subdiaphana (Carpenter) N. (S. limit)
Felaniella sericata (Reeve)—S.
Gari californica (Conrad)—N. (S. limit)
Hinnites multirugosus (Gale)—N.S.
Kellia laperousii (Deshayes)—N.
Lima dehiscens Conrad—S.
Lyonsia californica (Conrad)
Macoma yoldiformis Carpenter—N.
Nemocardium centifilosum (Carpenter)—Cal.
"*Nuculana acuta* (Conrad)"—N.S.
Semele incongrua Carpenter—Cal.
Solen sicarius Gould—N.S.
Trachycardium quadragenarium (Conrad)—Cal.

Polychaeta

Ammochares fusiformis (Delle Chiaje)—Cos.
Ampharete arctica Malmgren—N.
Arctonoe vittata (Grube)—N.S.
Diopatra ornata Moore—N.
Drilonereis filum (Claperede)—Cos.
Ephesia gracilis Rathke—Cos.
Eumida sanguinea (Oersted)—Cos.
Eunice siciliensis Grube—Cos.
Halosydna johnsoni (Darboux)—S.
Harmothoe imbricata (Linn.)—Cos.
Laonice cirrata (Sars)—Cos.
Lepidonotus coelorus Moore—N.
Lumbrinereis inflata (Moore)—N.
Malmgrenia nigralba Berkeley—N.
Nepthys dibranchis Grube—S. (N. limit)
Nereis callaona (Grube)—Cal.
Nereis neonigripes Hartman—Cal.
Nereis pelagica Linn.—Cos.
Nereis procera Ehlers (?)—N.
Odontosyllis parva Berkeley—N. (S. limit)
Phyllodoce medeirensis Langerhans—Cos.
Platynereis dumerillii var. *agassizi* (Audouin and Milne-Edwards)—N.S.
Podarke pugettensis Johnson—N.S.
Polydora giardi Mensil—Cos. (Reported only from France and Ireland)
Psammolyce spinosa Hartman—S.
Spirobranchus spinosus Moore—Cal.
Streblosoma bairdi (Malmgren)—N.
Stylarioides eruca (Claperede)—Cos.

Stylarioides inflata (Treadwell)—Cal.
Syllis gracilis Grube—Cos.

Amphipoda
Allorchestes sp.
Amphithoe humeralis Stimpson—N.S.
Amphithoe ramondi (Audouin)
Amphithoe scitula (Harford)
Amphithoe sp.
Ampelisca cristata Holmes—Cal.
Ampelisca lobata Holmes—Cal.
Ampelisca macrocephala Lilljeborg
Ampelisca venetiensis Shoemaker
Aoroides californica Alderman
Aoroides columbiae Walker
Aoroides sp.
Batea transversa Shoemaker
Bemlos macromerus Shoemaker
Caprella acutifrons Latreille
Caprella aequilibra Say
Caprella brevirostris Mayer
Caprella scaura Templeton—Cos.
Caprella sp.
Cheirimedon sp. (?)
Chevalia aciculae Walker
Eurystheus tenuicornis (Holmes)—N.
Hyale frequens (Stout)
Ischyrocerus sp.
Lembos concavus Stout
Melita fresnelii (Audouin)—Cos.
Neopleustes sp.
Photis californica Stout
Pleustes depressus Alderman
Sympleustes glaber (Boeck)

Isopoda
Idothea rectilinea Lockington—N.S.
Paracereis cordata Richardson—N. (S. limit)
Pentidotea resecata (Stimpson)—N.
Tanais normani Richardson—N.S.

Natantia
Crago holmesi (Rathbun)—S. (N. limit)
Crago munitella (Walker)—N.
Crago nigricauda (Stimpson)—N.S.
Hippolyte californiensis Holmes—N.
Pandalus guerneyi Stimpson—Cal.
Spirontocaris cristata (Stimpson)—N.
Spirontocaris lagunae Schmitt—Cal.
Spirontocaris palpator (Owen)—N.S.
Spirontocaris prionota (Stimpson)—N. (S. limit)
Spirontocaris snyderi Rathbun—N.S.

Repantia
Cancer jordani Rathbun—S.
Clythrocerus decorus Rathbun—S. (N. limit)
Clythrocerus planus (Rathbun)—S. (N. limit)
Erileptus spinosus Rathbun—S. (N. limit)
Heterocrypta occidentalis (Dana)—S.
Lophopanopeus heathi Rathbun—Cal.
Loxorhynchus crispatus Stimpson—N.
Pinnixa tomentosa Lockington—S. (N. limit)
Pinnotheres concharum (Rathbun)—N.S.
Podochela hemphillii (Lockington)—S.
Pugettia dalli Rathbun—N.S. (N. limit)
Pugettia richii Dana—N.S.
Scyra acutifrons Dana—N.

Pycnogonida
Anoplodactylus erectus Cole—Cal.
Nymphopsis spinosissimus Hall—Cal.
Palene pacifica Hedgpeth—Cal.
Pycnogonum sternsi Ives (?)—Cal.
Tanystylum californicum Hilton—Cal.

Echinoidea
Lytechinus anamesus H. L. Clark—N.

Holothuroidea
Cucumaria lubrica H. L. Clark—N. (S. limit)
Leptosynapta albicans (Selenka)—N.S. (Rare south of Pt. Conception.)
Pentamera pseudopopulifera Deichmann—S. (N. limit)

Ophiuroidea
Amphipholis squamata delle Chiajes—Cos.
Amphiura arcystata H. L. Clark—N.
Ophiopsila californica A. H. Clark—S. Cal. (N. limit)
Ophiothrix spiculata Leconte—S.

Tunicata
Eugyra n. sp.
This species of Eugyra is being described by Willard Van Name, American Museum of Natural History. He states in a communication that the species is closely related to *E. arluosa* (Alder & Hancock) of Northern Europe.
Molgula pugetiensis Herdman—N. (S. limit)
Molgula regularis Ritter—Cal.
Styela gibsii Stimpson—N.

FISHES COLLECTED ON AND NEAR SANTA CRUZ ISLAND

In the summer of 1934, August 27-29, Dr. Carl L. Hubbs, Scripps Institution of Oceanography, accompanied by R. S. Crocker and Donald H. Fry, collected 41 species of fishes in the waters surrounding Santa Cruz Island. With the kind permission of Dr. Hubbs the list of fishes is included in the present report. All of the information regarding the distribution of these species was received from Dr. Hubbs in a personal communication of December 26, 1940. On the basis of the information the distribution of each species is designated after the species in a manner followed in the invertebrate lists above.

The collecting stations and descriptive notes are also given below.

Station 151—Santa Cruz Island, at Albert Anchorage on south shore; at surface, over about 10 fathoms; spear and dip-net at night.

Station 154—Santa Cruz Island, at Cochies Prietos, on south shore; sandy beach, out to 2 fathoms depth, 150 feet from shore; beach seine, by day.

Station 155—Same locality; near surface over 5 to 6 fathoms; hook.

Station 156—Santa Cruz Island at west end, at west edge of Forney's Cove; sandy beach, out to 8 feet depth 100 feet offshore; beach seine, by day.

Station 157—Santa Cruz Island, at west end, on north face of Fraser Pt.; rocky tide-pools; poison.

Station 158—Santa Cruz Island, near west end, in Forney's Cove; surface to bottom (about 5 fathoms); hook.

Station 176—Santa Cruz Island, in cove at Diablo Pt. on north shore; 10 fathoms; hook.

Station 177—1 mile south of Anacapa Island, in about 40 fathoms.

Station 178—Anacapa Island on south side, just west of passage west of the eastern island; about 6 fathoms; dip-net, spear and hook.

LIST OF FISHES COLLECTED ON SANTA CRUZ ISLAND IN 1934

Prepared by Carl L. Hubbs, December, 1940

Aetobatus californicus (Gill): Station 154.
Tomales Bay, California, to central Lower California. —(S.)

Amphigonopterus aurora (Jordan and Gilbert): Station 157.
San Francisco region to Pt. Conception reefs, where mainland range is abruptly terminated (Hubbs, Biol. Bull., 40, 1921: 184).—(N.) (S. limit)

Amphistichus argenteus Agassiz: Stations 154, 156.
Bolinas Bay, California (records farther north are held to be erroneous) to San Diego.—(Cal.)

Atherinops affinis insularum (Gilbert): Stations 151, 155, 158, 178.
Northern and outer islands of the Channel Islands: replaced on Catalina Island, along mainland rocky coasts (but not the bays) and on Cedros Island by *A. a. cedroscensis*.—(S. Cal.)

Atherinopsis californiensis californiensis Girard: Stations 155, 158; other specimens in Museum from Smuggler's Cove, Santa Cruz Islands.
Northern Oregon (and possibly British Columbia) to northern Lower California; Santa Catalina Island.—(N.S.)

Ayresia punctipinnis Cooper [or *Chromis punctipinnis* (Cooper)]: Station 155; also in Museum some pelagic young from south of Santa Cruz Island (33° 52′ N., 199° 40′ W.).
Monterey, California, to Cedros Island, Lower California; also Santa Catalina and Guadalupe islands.—(S.)

Caulolatilus princeps (Jenyns): Station 158.
Monterey, California, to Lower California (and to Galapagos Island, assuming *C. anomalus* (Cooper) of Southern California is the same as *C. princeps*).—(S.)

Cebidichthys violaceus (Girard): Station 157.
Pt. St. George, near Crescent City, to Carpenteria, California (Hubbs, Pap. Mich. Acad. Sci., Arts and Letters, 7, 1927: 368).—(N.) (S. limit)

Cephaloscyllium uter (Jordan and Gilbert): Station 158.
Monterey to San Diego.—(Cal.)

Clinocottus analis: analis (Girard) x *australis* Hubbs (intergrades): Station 157.
Santa Barbara Channel and Ventura County and Santa Cruz Island (in Occ. Pap. Mus. Zool. Univ. Mich., 171, 1926: 10, I referred specimens from this region to *Clinocottus analis analis*, but now regard them as intergrades. The northern form, *C. a. analis*, ranges from Fort Bragg to the Pt. Conception reefs; the southern subspecies, *C. a. australis* Hubbs, from Pt. Fermin and Catalina Island to Lower California).

Crossochir koelzi Hubbs: Station 156.
Drakes Bay to San Diego (including paratypes from Santa Cruz Island).—(Cal.)

Cymatogaster aggregatus Gibbons: Station 154.
Southeastern Alaska to Todos Santos Bay, Lower California.—(N.S.)

Cypselurus californicus (Cooper): Stations 151, 178; also various other points to the south of Santa Cruz Island.
Pt. Conception and Santa Barbara Islands to Cape San Lucas.—(S.)

Dialarchus snyderi (Greeley): Station 157.
British Columbia to Pt. Loma.—(N.)

Embiotoca jacksoni Agassiz: Station 176.
San Francisco region (more northerly records were probably based on *Taeniotoca lateralis*) to Lower California, including offshore islands.—(N.S.)

Engraulis mordax mordax Girard: Stations 151, 158, 178.
Vancouver Island to Gulf of California.—(N.S.)

Epigeichthys atro-purpureus (Kittlitz): Station 157.
Southern Alaska to Point Arguello.—(N.) (S. limit)

Gibbonsia elegans: elegans (Cooper) x *montereyensis* Hubbs (intergrades): Station 157.
Hitherto known (See Hubbs, Pap. Mich. Acad. Sci. Arts and Letters, 7, 1927: 353-63) from outer coast of Santa Barbara County (at points Sal, Arguello and Conception); *G.e. montereyensis* ranges from northern California (one British Columbia record but none from Washington or Oregon) through San Luis Obispo County; *G.e. elegans* from Carpenteria to northern Lower California (including Catalina Island).

Gibbonsia metzi Hubbs: Stations 156, 157.
Entire length of California coast.—(Cal.)

Girella nigricans (Ayres): Station 157.
Monterey (rare) to Cape San Lucas and Gulf of California; including offshore islands.—(S.)

Heterostichus rostratus Girard: Station 156.
San Francisco to near Los Coronados Islands, and Guadalupe Island.—(S.)

Hyperprosopon argenteum Gibbons: Stations 154, 156.
British Columbia to northern Lower California.—(N.S.)

Hypsoblennius gilberti (Jordan): Stations 151, 178.
Santa Barbara (and islands), California, to Todos Santos Bay, Lower California; Santa Catalina Island. —(S.) (N. limit)

Micrometrus minimus (Gibbons): Station 156.
Duxbury Reef in San Francisco region to Lower California, including Channel Islands.—(S.)

Montereya recalva (Greeley): Station 157.
San Francisco Peninsula to reef at Pt. Conception, and Los Coronados Islands; presumably absent along Southern California mainland (Hubbs, Occ. Pap. Mus. Zool. Univ. Mich., 171, 1926: 17).—(Cal.)

Oxyjulis californica (Gunther): Station 158.
Monterey to San Diego; also Santa Catalina, Cedros and Guadalupe islands.—(S.)

Paralabrax clathratus (Girard): Stations 158, 178.
San Francisco to Cape San Lucas; including Channel Islands.—(S.)

Paralichthys californicus Ayres: Station 158.
Tomales Bay to San Diego (more southern records were likely based on other species).—(Cal.)

Pimelometopon pulcher (Ayres): Station 158.
Monterey (rare) to Southern and Lower California.—(S.)

Pneumatophorus diego (Ayres): Stations 151, 178.
Southern Alaska to Magdalena Bay, Lower California, and farther to either Gulf of California or Cape San Lucas.—(N.S.)

Sardinops caerulea (Girard): Stations 151, 158.
British Columbia (there may be a recent Alaska record too) to Gulf of California.—(N.S.)

Sebastodes atrovirens (Jordan and Gilbert): Station 158.
Point St. George, northern California to San Martin Island, Lower California.—(N.S.)

Sebastodes chrysomelas (Jordan and Gilbert): Station 178.
Puget Sound to San Diego.—(N.)

Sebastodes rastrelliger (Jordan and Gilbert): Station 158.
Humboldt Bay to San Diego.—(N.)

Sebastodes serranoides Eigenmann and Eigenmann: Stations 158, 177, 178.
San Francisco to Cape Colnett, Lower California.—(S.)

Sebastodes vexillaris Jordan and Gilbert: Station 158.
Central California to Cape Colnett, Lower California.—(S.)

Syngnathus californiensis californiensis Storer: Stations 151, 156.
Offshore waters, central California, to Ballenas Bay, Lower California (Herald, Allan Hancock Pac. Exp., 9, 1940: 61).—(S.)

Taeniotoca lateralis (Agassiz): Station 158.
British Columbia to Pt. Arguello (the record from San Benito Island, Lower California, was based on *Embiotoca jacksoni*).—(N.) (S. limit)

Trachurus symmetricus (Ayres): Stations 151, 154, 178.
Monterey to San Diego (and beyond to Chile, according to some); Santa Catalina and Guadalupe islands.—(S.)

Ulvicola sanctae-rosae Gilbert and Starks: Station 158.
Known only from the Channel Islands (hitherto reported from Santa Rosa and Catalina) and Guadalupe Island.—(S.) (N. limit)

Xererpes fucorum (Jordan and Gilbert): Station 157.
Puget Sound to Pt. Loma, including Channel Islands.—(N.)

DISCUSSION

A total of 529 marine species are considered in this report, including the 41 species of fishes collected by Dr. Hubbs.

The information obtained on the distribution records of the marine animals collected on Santa Cruz Island is not uniform and in many instances is incomplete. More specific records of the ranges of the organisms are not available to the author at the present time.

Table 2 gives a summary of the distribution records which were obtained for 491 species of animals collected on Santa Cruz Island. The organisms are placed in three categories, intertidal species, subtidal species, and fishes. On the basis of distribution data these groups are arbitrarily classified according to the ranges of the organisms along the eastern shore of the Pacific. The abbreviations used to designate the groups are explained above under the phylogenetic lists: N—Northern; S—Southern; N.S.—Northern and Southern; S. Cal.—Southern California south of Point Conception; Cal.—limited to the California coast; Cos.—Cosmopolitan, not limited to the Pacific Ocean.

TABLE 2. Summary of distribution records of animals collected on Santa Cruz Island.

	N.		S.		N.S.		S. Cal.	
	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent
Intertidal	91	30.3	75	25.3	63	21.6	6	2.0
Subtidal	42	27.6	36	23.9	30	19.8	4	2.6
Fishes	8	20.5	16	41.0	8	20.5	1	2.5
Total	141	28.7	127	26.0	101	20.9	11	2.2

	Cal.		Cos.		N. limit		S. limit	
	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent
Intertidal	48	16.0	14	4.6	35	11.6	34	11.3
Subtidal	25	16.2	15	9.9	19	12.5	13	8.5
Fishes	6	15.3	..	...	2	5.0	4	10.0
Total	79	16.1	29	5.9	56	11.4	51	10.3

The numbers of species and the percentages of the totals of the species of each category are given under each group. In the last four columns of the table are presented the numbers and percentages of the species which have northern or southern limits of their ranges in the vicinity of Santa Cruz Island. There is a relatively equal percentage of northern (28.7%) and southern (26.0%) species found in the island waters. A total of 21.7% of the organisms reach the limits of their ranges along the California coast in the region of Santa Cruz Island. These data give further evidence that the island is located in a transition area between the northern and southern faunas. Detailed distribution studies of the mainland coastal faunas at points north and south of Santa Cruz will be necessary to indicate more clearly the location of the barrier which appears to exist in this coastal region.

The studies of Santa Cruz Island have extended the ranges of the following species:

Hydrozoa
Abietinnaria amphora
Bimeria pusilla
Sertularella erecta

Bryozoa
Alcyonidium polyoum
Crassimarginatella tincta
Crisia pacifica
Dendrobeania laxa
Diaperoecia palmata
Holoporella hexagonalis
Lagenipora erecta
Membranipora membranacea
Smittina collifera
Thalamoporella gothica var. *prominens*
Tricellaria erecta
Tricellaria occidentalis var. *catalinensis*

Amphineura
Tonicella liniata

Gastropoda
Odostomia (Evalea) angularis

Polychaeta
Ephesia gracilis
Lumbrinereis latreilli
Malmgrenia nigralba
Nephthys dibranchis
Odontosyllis parva
Odontosyllis polycera
Phyllodoce madeirensis
Polydora giardi
Streblosoma bairdi
Syllis fasciata
Syllis gracilis
Syllis hyalina
Trypanosyllis gemmipara

Isopoda
Aega leconti

Natantia
Periclimenes tenuipes

Reptantia
Lepidopa myops
Petrolisthes cinctipes

Pycnogonids
Eurycyde spinosa

Holothuroidea
Cucumaria lubrica
Parastichopus parvimensis
Pentacta trachyplaca
Pentamera pseudopopulifera
Thyone rubra
Thyonepsolus nutriens

Ophiuroidea
Ophiactis simplex
Ophiopsila californica

Tunicata
Amaroucium aequali-siphonis
Clavellina huntsmani
Didemnum carnulentum
Molgula pugetiensis
Molgula regularis
Styela (Katatropa) vancouverensis

Although extensive shore collecting has been done along the California coast in the past, several specimens apparently new to science were obtained in the Santa Cruz Island material. A new species of hydroid, *Plumularia paucinema* has been described by Fraser (1940, p. 42). An unknown species of Pseudomelatoma is being studied by Myra Keen. Another gastropod which appeared to represent a new genus is, according to a late communication from Dr. Keen, "very close to the genotype of Episcynia, a genus hitherto restricted to the Caribbean." A new species of Lyonsia was also found in the collections.

Two new species of Petrolisthes have been described in a manuscript of Steve A. Glassell. Dr. S. S. Berry is studying an apparently new chiton of Chaetopleura (Pallochiton). Ten species of amphipods, as yet unidentified, are in the collections sent to Clarence R. Shoemaker. Dr. Van Name reports a new species of the tunicate Eugyra in the Santa Cruz material.

SUMMARY

The littoral and shallow water marine invertebrates of Santa Cruz Island were collected in the summer of 1939. Studies were made at six shore stations which appear to be representative of the entire coast of the island. The characteristic faunas of the varied shore habitats are described. Systematic faunal lists are given for each station. In addition to the shore collecting, shallow dredgings were obtained at ten localities in the island waters.

In order to make the studies of the Santa Cruz Island faunas more complete the writer was permitted to include some unpublished notes on a collection of fishes made by Dr. Carl Hubbs, Scripps Institution of Oceanography in the summer of 1934.

The available records of the ranges of the organisms are given and discussed. These data give further evidence supporting the view that a faunal barrier exists in the coastal waters of this region of California.

The ranges of 49 species of marine invertebrates were appreciably extended by the studies. Several undescribed species were found in the collections.

BIBLIOGRAPHY

Bartsch, P. 1921. Ocean currents, the prime factor in the distribution of marine mollusks on the west coast of America. Spec. Publ. Bernice P. Bishop Mus. **7:** 505-526.

Berkeley, E. & C. 1941. On a collection of Polychaeta from Southern California. Bull. So. Calif. Acad. Sci. **40:** 16-20.

Bremner, Carl St. J. 1932. Geology of Santa Cruz Island, Santa Barbara County, California. Santa Barbara Mus. Nat. Hist. Occas. Pap. **1:** 5-33.

Cockerell, T. D. A. 1938. San Miguel Island, California. Sci. Mo. **46:** 180-187.

1938. Studies of island life. Univ. Colo. Studies **26:** 3-20.

Dall, W. H. 1909. Report on a collection of shells from Peru with a summary of the littoral marine Mollusca of the Peruvian zoological province. Proc. U. S. Nat. Mus. **37:** 147-294.

1921. Summary of the marine shell bearing mollusks of the northwest coast of America, from San Diego, California to the Polas sea, etc. U. S. Nat. Mus. Bull. **112:** 1-217 pages.

Dana, J. D. 1853. Crustacea: United States exploring expedition. Pt. II, **14:** 1-1618.

Fraser, C. McLean. 1938. Hydroid distribution in the North Eastern Pacific. Trans. Roy. Soc. Canada **32:** 39-42.

1940. Some hydroids from the California coast, collected in 1939. Trans. Royal Soc. Canada Ser. III (5): 34-44.

Hewatt, Willis G. 1935. Ecological succession in the Mytilus californianus habitat as observed in Monterey Bay, California. Ecology **16:** 244-251.

1937. Ecological studies on selected marine intertidal communities of Monterey Bay, California. Amer. Mid. Nat. **18:** 161-206.

1938. Notes on the breeding seasons of the rocky beach fauna of Monterey Bay, California. Proc. Calif. Acad. Sci. **23:** 282-288.

1940. Observations on the homing limpet, Acmaea scabra Gould. Amer. Mid. Nat. **24:** 205-208.

Keen, A. Myra. 1937. An abridged check list and

bibliography of West North American marine Mollusca. Stanford Univ. 1-87.

Kitching, J. A. 1935. An introduction to the ecology of intertidal rock surfaces on the coast of Argyll. Trans. Roy. Soc. Edin. **58:** 351-374.

Scofield, Eugene C. 1934. Early life history of the California sardine (Sardina caerulea), with special reference to distribution of eggs and larvae. Calif. Div. of Fish & Game. Fish Bull. **41:** 1-48.

Schenck, H. G., & Myra Keen. 1936. Marine molluscan provinces of Western North America. Proc. Amer. Phil. Soc. **76:** 921-938.

Smith, J. P. 1919. Climatic relations of Tertiary and Quaternary faunas of the California region. Proc. Calif. Acad. Sci. (4) **9:** 123-273.

Steinbeck, John, & Edward F. Ricketts. 1941. Sea of Cortez. New York 1-598.

Sverdrup, H. U., & W. E. Allen. 1939. Distribution of diatoms in relation to the character of water masses and currents off Southern California in 1938. Sears Found. Jour. Mar. Res. **2:** 131-144.

Sverdrup, H. U., & R. H. Fleming. 1941. The waters off the coast of southern California March to July, 1937. Bull. Scripps Inst. Oceanogr. **4:** 261-378.

Tibby, Richard B. 1939. Report on returns of drift bottles released off Southern California, 1937. Div. Fish & Game. Fish Bull. **55:** 5-36.

A COLLECTION OF SHRIMPS FROM SANTA CRUZ ISLAND, CALIFORNIA[1]

WALDO L. SCHMITT

The shrimps (Decapoda Natantia) here reported upon were collected by Dr. Willis G. Hewatt and his assistant, Woodbridge Williams, in the course of an ecologic survey of Santa Cruz Island in the summer of 1939. Though the collection is not a large one, comprising only 15 species, it contained two species of particular interest: *Spirontocaris carinata* (Holmes), a species of which the Museum formerly had but a single specimen and of which there seem to be very few specimens in existing collections; and *Palaemon tenuipes* (Holmes), which has made it possible to clear up an apparent discrepancy between a figure of one of its chelae published by Miss Rathbun (1904, Harriman Alaska Exped., vol. 10, p. 34, fig. 12) and the original description of Holmes (1900, as *Anchista tenuipes,* Occ. Paps. Calif. Acad. Sci., vol. 7, p. 216).

Most of the specimens were of small size, giving the impression that less fully developed individuals were taken in the course of the collecting. Nevertheless, eight of the fifteen species are represented wholly or in part by ovigerous females. On the other hand, the single specimen of *Spirontocaris lagunae* and the two of *Periclimenes tenuipes* are the largest individuals of their respective species that I have ever seen. One day's collecting seems to have been devoted to each of four of the five general localities investigated; four days to the fifth, Scorpion Harbor, where, as a result, twelve species were secured as compared with from two to five species at each of the other localities.

Figures and descriptions of all fifteen species mentioned in this report will be found in one of the five well known works dealing wholly or in part with the crustacea of California, including Rathbun and Holmes, cited above, and the following:

Johnson, Myrtle E., & Harry J. Snook. 1927. Seashore animals of the Pacific Coast. N. Y.

Ricketts, Edward F., & Jack Calvin. 1939. Between Pacific Tides. Stanford Univ. xii + 320.

Schmitt, Waldo L. 1921. The Marine Decapod Crustacea of California. Univ. Calif. Pub. Zool. **23:** 1-470.

ANNOTATED LIST OF SPECIES

Periclimenes tenuipes (Holmes)

Rock slide between Pelican Bay and Prisoner's Harbor; July 17 .... 2 ovig.

This species is rarely taken in the waters of the state. I have seen a single specimen from Catalina Island and three others bearing only the designation "southern California." From the Gulf of California I have seen six specimens, of which two are ovigerous. The two specimens that Dr. Hewatt collected and presented to the National Museum are welcome additions to the national collections, not only because they are large and well preserved specimens, but also because the only leg of the second pair in the vial with them had the same relative length of the fingers of the second pair as described by Holmes (*op. cit.*, p. 216), about two-thirds the length of the palm. This is at variance with the Lower California specimen figured by Miss Rathbun (*op. cit.*, p. 34, Fig. 12), in which the fingers are about half the length of the palm.

An examination of the National Museum material showed that most of the specimens were incomplete except one ovigerous female from the Patos Island anchorage, Gulf of California, a gift of the California Academy of Sciences, which had both legs of the second pair present. As in most, if not all, palaemonids which have the larger chelate legs of the second pair asymmetrical, the larger, longer, and stouter chela has the fingers but half the length of the palm, and the less stout, shorter chela has the fingers almost exactly two-thirds the length of the palm. (Holmes described a minor cheliped; Miss Rathbun figured a major one.) Dr. Hewatt's two specimens, the largest I have seen, are each about 25 mm. long, with carapace and rostrum together measuring 10 mm. In Miss Rathbun's figured specimen the carapace and rostrum together measure about 8 mm., and in the Patos Island specimen 7.

[1] Published by permission of the Secretary of the Smithsonian Institution.

Pandalus platyceros (Brandt)

Pelican Bay, dredged; 25 fms.; rock bottom, July 11. 2

The larger of these two specimens measured 45 mm. in length from the tip of the rostrum to the end of the telson, the smaller 26 mm. Fully developed *P. platyceros* will attain a length of from 138 to 214 mm. or more.

Pandulus gurneyi (Stimpson)

Scorpion Harbor; 5 fms.; June 26 1
Prisoner's Harbor; 15 fms.; July 27 2

The first of these specimens is 33 mm. long; the last two about 17 and 33 mm. Better developed individuals of this species will measure between 70 and 80 mm. in length.

Hippolyte californiensis Holmes

Scorpion Harbor, dredged; 2-3 fms.; June 25 .... 7 (6 ovig.)
Scorpion Harbor; July 4 .... 1 ovig.

The five specimens with complete rostra have the usual, not the atypical, arrangement of teeth figured by Holmes (*op. cit.*, p. 193, pl. 2, fig. 38; *cf.* Schmitt 1921, p. 48, and Rathbun 1904, p. 56). Counting the subapical teeth, the rostral formula for the July 4th specimen is $\frac{3}{5}$; for the June 25th specimens, $\frac{3}{3}$, $\frac{3}{4}$, $\frac{3}{4}$, $\frac{4}{5}$.

Spirontocaris prionota (Stimpson)

Scorpion Harbor; 5 fms.; June 26 1
Pelican Bay; 25 fms.; rock bottom, July 11 2

The largest of the three specimens measure 17 mm. in length, a little less than half as long as the 35 mm. long type specimen.

Spirontocaris snyderi Rathbun

Scorpion Harbor; 20 fms.; June 26 .... 1 ovig.

This 25 mm. long specimen lacks a considerable part of the rostral blade, but otherwise is readily to be identified as this species; it is but 3 mm. shorter than the type of the species.

Spirontocaris lagunae Schmitt

Scorpion Harbor; 5 fms.; June 26 .... 1 ovig.

This specimen is 4 mm. longer than the 20 mm. long type of the species.

Spirontocaris carinata (Holmes)

Scorpion Harbor; July 4 2

Although Holmes noted that the species was dredged in Monterey Bay in large numbers in November 1895, these are the first to come to the National Museum since Miss Rathbun (*op. cit.*, p. 84) extended its range southward to off Point Loma. Later one specimen taken in Monterey Bay and two from Fort Bragg were presented to the Museum by Dr. Walter K. Fisher from the collections of the Hopkins Marine Station at Pacific Grove. Dr. Hewatt's specimens appear to be juvenile males, each about 19.5 mm. in length; the Point Loma specimen is a female about 48 mm. long; while the Fort Bragg specimens are 37.5 and 41.5 mm. and the Monterey specimen 53.5 mm. long. The last and largest of these is an ovigerous female. In this fully developed specimen the carapace is relatively small as compared with the rest of the body. The rostrum of this specimen is a little shorter than the carapace, but in each of the others the rostrum is equal to the carapace in length or a little longer. It almost seems that Holmes' original description is primarily that of a male, while his figure, as stated, is that of a female. It may be noted that the tip of the lateral spine at the antero-inferior angle of the carapace is as far behind the convex anterior margin of the carapace as the tip of the antennal spine extends beyond the margin. The number of dorsal rostral teeth of the five specimens at hand are 5 or 6; the ventral 3-6. The two Scorpion Harbor specimens and the ovigerous female from Pacific Grove have the same number of teeth above and below, $\frac{5}{5}$, $\frac{6}{6}$, and $\frac{5}{5}$ respectively; the other two Pacific Grove specimens had $\frac{5}{3}$ and $\frac{6}{4}$; the Point Loma specimen $\frac{5}{4}$.

Spirontocaris palpator (Owen)

Scorpion Harbor, dredged; 2-3 fms.; June 25 .... 3 (2 ovig.)
Scorpion Harbor; 5 fms.; June 26 ... 25 (10 ovig.)
Scorpion Harbor; kelp beds; July 5 .... 1 ovig.
Pelican Bay; 25 fms.; rock bottom; July 11 1
Pelican Bay; 5-10 fms.; July 12 .... 3 ovig.
Rock slide between Pelican Bay and Prisoner's Harbor; July 17 5
Prisoner's Harbor; 15 fms.; July 27 ... 15 (9 ovig.)
Willow Harbor; low tide (-4); July 30 ... 1 ovig.
Willow Harbor, dredged; 7 fms.; July 30 ... 1 ovig.

Spirontocaris picta (Stimpson)

Scorpion Harbor; July 4 2
Scorpion Harbor; outlying island, rocks to east; July 4 1
Rock slide between Pelican Bay and Prisoner's Harbor; July 17 5

Spirontocaris cristata (Stimpson)

Scorpion Harbor; 5 fms.; June 26 1
Pelican Bay; 25 fms.; rock bottom, July 11 .... 6 (4 ovig.)

Crangon clamator (Lockington)

Rock slide between Pelican Bay and Prisoner's Harbor; July 17 .... 5 (2 ovig.)
Willow Harbor; low tide (-4); July 30 3

As J. C. Armstrong (Amer. Mus. Novitates, No. 1096, p. 1, 1940) points out, Lockington's *C. clamator* is not to be synonymized with Guérin's *C. dentipes*, a distinct European species, as a number of authors, including myself, have done in the past.

Crago nigricauda (Stimpson)

Scorpion Harbor; kelp beds; [July 5 ?] 1
Scorpion Harbor; July 5 (with rhizocephalan parasite) 1
Prisoner's Harbor; ½ mile off shore; 20 fms.; July 27 1

These three specimens, in order, as 20, 38, and 25 mm. long.

Crago holmesi (Rathbun)

Scorpion Harbor; 1 fms.; June 26 2
Scorpion Harbor; kelp beds; [July 5 ?] 2
Prisoner's Harbor; ½ mile off shore; 20 fms.; July 27 .... 1 ovig.

The ovigerous female is about 3 mm. longer than the type specimen, which measured 23 mm. However, there is a larger specimen, also an ovigerous female, in the national collections from Laguna Beach, a gift from Dr. Wm. A. Hilton, measuring about 28 mm. The other four specimens of *C. holmesi* in Dr. Hewatt's collection ranged from about 17 to 21 mm. in length.

Crago munitella (Walker)

Scorpion Harbor; 7 fms.; June 26 1
Prisoner's Harbor; 15 fms.; July 27 .... 4 (3 ovig.)
Prisoner's Harbor; ½ mile off shore, 20 fms.; July 27 .... 1 ovig.

These six specimens ranged from 12 to 19 mm. in length. The type of this species measures 25 mm.

PHYTOSOCIOLOGY OF THE PRIMEVAL FOREST IN CENTRAL-NORTHERN WISCONSIN AND UPPER MICHIGAN, AND A BRIEF POST-GLACIAL HISTORY OF THE LAKE FOREST FORMATION

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PHYTOSOCIOLOGY OF THE PRIMEVAL FOREST IN CENTRAL-NORTHERN WISCONSIN AND UPPER MICHIGAN, AND A BRIEF POST-GLACIAL HISTORY OF THE LAKE FOREST FORMATION[1]

PART I. THE FOREST SURVEY

Introduction

The transition forest wedged between the two great formations known as eastern deciduous and boreal forests has perhaps been discussed more than any other forest formation on the North American continent. Though a number of names have been suggested (Nichols, 1935) and used to designate it, the name most commonly applied is the one proposed by Weaver and Clements (1938), "lake forest." The formation is characterized by two, at times sharply, separated associations. On sandy soil it is coniferous forest composed primarily of *Pinus strobus* and *P. resinosa,* with successional stages in dry habitats dominated almost entirely by a consocies of *Pinus banksiana.* On the better loam and clay soils the forest consists of an association formed by *Tsuga canadensis* and *Betula lutea,* together with some representatives of the eastern deciduous forest, especially *Acer saccharum* and, eastward of central Wisconsin, *Fagus grandifolia.* This latter part of the lake forest is customarily referred to as northern hardwoods. The tree stratum of relic colonies in bogs and lowlands is dominated by genera which are characteristic in the boreal forest; Abies, Picea, and Larix. Of these associates *Abies balsamea* forms at times the small tree stratum in stands controlled by *Pinus strobus.* This is true at least in the central northern part of Wisconsin, westward of Lake Michigan (Tables 1 and 2). In upper Wisconsin, westward of Lake Michigan, the association complex of the northern hardwoods is simplified by the disappearance of *Fagus grandifolia.*

From the middle of the last to the beginning of the present century the lake forest was decimated by the lumbering activity and by extensive forest fires. The result is that today much of the vast region is vegetated by small shrubs, or by aspen and *Pinus banksiana* subclimax forest. According to Shirley (1941) such aspen and shrub vegetation today occupies some 18.5 million acres in the upland areas of the Lake States.

Very little work is on record which presents quantitative and qualitative data on the sociology of the arboreal layer in the primeval forest of these states. For that reason the present study was undertaken while the author was a member of the Wisconsin Geological and Natural History Survey at the Limnological Station in Vilas County during the summer of 1940. An excellent opportunity presented itself at the time to study several small as well as large tracts of undisturbed forest in Vilas and Price Counties, Wisconsin, and in Gogebic County, Michigan.

The three counties included in this study are grouped about the Wisconsin-Michigan state line in the north-central part of Wisconsin (Fig. 1). The region is typical glaciated terrain with rolling morainal and dissected drift topography. Lakes, bogs, and wet lowlands are characteristic surface features. The soil is for the most part loose sand and gravel, or sand and gravel mixed with clay. The latter constitutes the better loam and clay soils of the region, and it is this soil which civilized man, when he came, found almost universally covered by northern hardwood forest.

It is with gratitude that I acknowledge the opportunity to serve on the staff of the Wisconsin Geological and Natural History Survey during the summer of 1940; it enabled me to make the field observations involved in this study; thanks are also expressed to the Wisconsin Alumni Research Foundation whose grant of funds made the forest survey possible. Mr. Martin J. Gillen was a most generous host, and his keen interest in the work was a stimulating influence while the field studies were in progress. The many helpful suggestions and the friendship of the late Professor Chancey Juday are fond memories. Thanks is also expressed to Miss Emily Helming, professor of English at Butler University, for critical reading of and corrections suggested for the major part of the manuscript.

Plan of Study

The aim of the study was to include representative stands of primeval forest, and also a number of disturbed forests with pronounced secondary succession. It was found possible to survey two stands of pine and eight stands of the northern hardwoods type; two of the latter are in the process of rebuilding after cultural disturbances. In a minor way, a study was made of the role played by decaying logs in the establishment of the dominant species (Table 21).

Areas Included

The Pine Forest

One of the two stands of pine forest included covers approximately 40 acres in the Northern Highland State Forest at Trout Lake, Vilas County, Wisconsin. It occupies the peninsula formed by the upper sections of Trout Lake, T. 41 N., R. 6 E., Sec. 7. A part of the stand was disturbed in the past when part of the area adjacent to the lake served as a tourist camp. Most of it, however, is relatively

[1] Contribution 164 from the Botanical Laboratory of Butler University, Indianapolis, Indiana; and notes and reports 116 from the Limnological Laboratory of the Wisconsin Geological and Natural History Survey, University of Wisconsin.

free of cultural disturbances. The trees are tall; many of them are evenaged (approximately 155 years), with small crowns (Figs. 2 & 3), which make for low percentage of coverage in the forest canopy.

The second stand is a beautiful tract of 60 to 80 acres between Big Crooked and Wolf Lakes on the property of the Dairymen's Country Club, T. 42 N., R. 6 E., Sec. 6, from which the name Dairymen's Country Club forest was derived (Fig. 4). It is one of the most magnificent stands of pines the writer has seen since his boyhood days in Presque Isle County, Michigan. The trees are free of fire scars, and the vegetation has been left to develop without interference and according to natural laws. The crown cover is controlled chiefly by *Pinus strobus* (Fig. 4) and to a lesser degree by *Pinus resinosa*.

Crown coverage is only about 85 percent. The trunks of the trees are tall and straight; they terminate in a medium-sized crown. The crowns are somewhat fuller than those in the Point Forest, but permit considerable light to penetrate to the floor. To the west the pines gradually yield to typical northern hardwoods (Table 24). The second layer tree stratum consists primarily of *Acer rubrum* and *Abies balsamea* (Table 1).

The Northern Hardwoods

The eight stands included in the study of northern hardwoods were distributed over a wider area than the pine forests, and for that reason hardwoods yielded, perhaps, more reliable data on the fidelity of certain key species in the crown cover than the pine forests.

The Caro Woods is a magnificent stand of hardwoods comprising about 80 acres along the eastern shore of Pike Lake, T. 39 N., R. 3 E., Sec. 1, in Price County, Wisconsin. Unfortunately it has been somewhat "cleaned up" by removal of fallen logs, which no doubt will have its influence on natural reproduction in the future. The trees are tall, and their crowns form a closed canopy with a coverage of 90 to 100 percent (Fig. 5). The topography is of the semi-lowland type with low ridges entering at several places.

The Chequamegon National Forest stand is very mature. Its location is T. 38 N., R. 3 E., Sec. 12, Price County, Wisconsin. One might be justified to describe it as an association of dying old trees and dense undergrowth of young trees. Windfall is severe, and this permits more light to penetrate to the forest floor than in the Caro Woods. Under the existing conditions root competition from old trees must be greatly reduced, permitting development of a dense growth of young trees. The area comprises about 40 acres.

The most extensive stand included in the study was the Marathon Corporation northern hardwoods. It begins about six miles north of the Michigan-Wisconsin state line. The quadrat study (Tables 13 & 14) was made 1.5 miles south of highway 2, Gogebic County, Michigan, along the fire lane road to the Gillen Nature Reserve. The topography is slightly rolling, but a considerable portion is of the semi-lowland type, merging into adjacent bogs. According to a personal communication from Mr. J. S. Landon of the Marathon Corporation, the forest totals 13,000 acres.

The stand located between Roach and Tenderfoot Lakes (T. 43 N., R. 8 E., Sec. 7) along the Michigan-Wisconsin state line on the Gillen Nature Reserve is designated as Roach Lake Forest. It occupies a shallow valley which in early post-glacial times contained, perhaps, a narrow arm of water connecting Roach and Tenderfoot Lakes. Ridges of moderate relief extend into the valley at a number of places, affording opportunity to study variation in the importance of a number of key species within an otherwise similar stand.

Several miles south of the previously described woods, also on the Gillen Nature Reserve, is another stand of northern hardwoods which has seen little cultural disturbance. The area is an upland above the deep-set Potzger Bog, which slopes gradually into the valleys leading to Palmer Lake. For convenience it has been designated as Potzger Bog Forest. The exact location is T. 43 N., R. 8 E., Sec. 8.

Lumbering left its imprint on a stand of about 80 acres north of Forest Lake in Vilas County, Wisconsin, T. 42 N., R. 8 E., Sec. 5. Cutting was apparently limited to the larger stems, for the woods has all the appearances of a primeval forest. Here was an opportunity to study the effect of slight disturbance and the process of rebuilding according to natural laws. The topography slopes from a comparatively high, flat ridge to a small lake in the last stages of filling. The crowns of the trees form a closed canopy, so that ground cover in the Forest Lake stand is sparse.

On the grounds of the Dairymen's Country Club, previously referred to, is also a stand of hardwoods, designated as Dairymen's Country Club Hardwoods. This forest shows no evidence of cultural disturbance in the recent past, but the vitality of the stand is low. Windfall is abundant. The habitat is a low plateau between Wolf and Big Crooked Lakes, about a half mile west of the white pine forest described earlier.

The Scaffold Lake Forest was included in the study specifically for the sake of a comparison of secondary succession with rebuilding according to natural laws. The topography about Scaffold Lake is a high, little dissected upland sloping to the lake and to a number of bogs (T. 40 N., R. 6 E., Sec. 8). The original timber was clear cut, and subsequent fires must have denuded the area completely. The trees are all very young (Table 20), and form a dense crown cover in which even isolated old trees are wanting.

Methods

The sampling unit employed in the forest survey was 100 square meters. The number of such units taken varied from 10 to 50. A stout cord with loops at each ten-meter section delimited the quadrat. The loops could easily be slipped over wooden stakes to

outline a square. A skip of ten meters followed each quadrat sample, except in the line transect recorded in Table 24. In each stand one or more one-eight acre plots were laid off and all stems one inch or larger in diameter were measured for diameter, and counted; young trees above a meter in height but below one inch D.B.H. (diameter breast high) were also counted. Sociological features considered in the study were frequency, density, fidelity, and basal area. One strip transect (Table 24) ten meters in width, was run from the hardwoods to the adjacent pine stand on the Dairymen's Country Club property in order to study transitional features between these two types of forest cover. D.B.H. measurements were made with wooden calipers. The ground cover received special consideration only in the pine stands of the Dairymen's Country Club forest, on the basis of 20 one-meter quadrats (Table 23). Seedlings and small trees growing on 55 decaying logs, in six different stands, were listed (Table 21). The quadrat unit for this work was 36 inches by diameter of the trunks. The specific purpose was to determine in a general way the part played by decaying logs in the primeval forest with respect to seedling establishment.

For the pollen analysis the following techniques were employed: The samples of sediments from bogs were taken with a Hiller type borer and of lakes with the new Wilson borer (for complete description see Wilson, 1941). Samples sufficient to fill a 2-ounce bottle were as a rule taken at foot-level intervals. The borers were washed carefully after each sample taken. The bottles were labelled with location and foot-level, then stoppered tightly. In the laboratory a knife-tip size pellet from the field sample was placed into 10 cc. of 95 percent alcohol, and with the aid of a camel's hair brush the material was separated. The beaker was tilted slightly for about a half minute to permit settling out to one side of the larger inorganic and organic particles. Five minutes or more were given for settling out of the fine particles. The sediment was then drawn into a pipette and a drop placed on a microscope slide. The alcohol was permitted to evaporate until the sediment was barely moist. Then warm glycerine jelly was added, and with the aid of a scalpel glycerin and sediment were thoroughly stirred up and a cover glass added. With aid of a mechanical stage and 640 X magnification, a count of 200 pollen grains was tabulated from each foot-level. Expressed in terms of percentage of the total count, each genus is shown on the graphs which represent Figures 6 to 30 in this study.

A re-count was made of Picea and Abies pollens for Figs. 6, 7, 9, 11, and 14 to correct an error with respect to these two genera as reported in the original publications.

OBSERVATIONS AND RESULTS

IN THE PINE STANDS

Climax pine forest is represented by two variants, which are determined by either one of the two dominant species; ***Pinus strobus*** **or *P. resinosa*. Habitat sites control degree of prominence in the crown cover of either one of these two species. The moist lowland areas favor control by *Pinus strobus,* whereas,** sandy, elevated areas and ridges favor *P. resinosa.* Of the two stands studied, the Dairymen's Country Club forest represents a good example of the *Pinus strobus* cover type (Tables 1 & 2); the Point Woods along Trout Lake is a typical *Pinus resinosa* cover type (Tables 3, 4). Woody species associated as small-tree stratum vary in the two cover types. *Abies balsamea* is a more persistent associate in the *Pinus strobus* variant (Tables 1 & 2), and *Quercus borealis* var. *maxima* in the *Pinus resinosa* variant (Tables 3 & 4). Broadleaved species show a comparatively vigorous reproduction under the crown cover of the conifers, but apparently cannot develop to maturity in the shade (Tables 1 & 3). The greatest abundance and highest frequency are shown by *Acer saccharum* and *A. rubrum,* and in the *Pinus resinosa* type also *Quercus borealis* var. *maxima* (Table 3). Corylus is the only shrub of any importance in both types of coniferous forest (Tables 1 & 3).

More species enter into the sociology of the pine associations than into that of the deciduous forest, as Tables 1, 3, 6, 9, 11, 13, 15, 16, and 18 show. In most instances the pine associations have double the number of woody species of that found in the deciduous forest. It is very probable that light plays a prominent role in determination of this difference. The crown cover of the pine stands is open, perhaps only 85 percent coverage, while the crowns of the trees in the deciduous forest form a closed canopy. The greater penetration of light evidently enables even Quercus to invade the pine forest (Tables 3 & 4), constituting a fairly well expressed second layer tree stratum in the *Pinus resinosa* type. However, Quercus is always in the small-size classes; mortality evidently runs high when, after years of suppressed growth, overtopping of the taller pines is not achieved. The secondary status of Quercus in northern Wisconsin and Michigan is evidently a climatic control, not only is the genus limited to the pine association, a characteristic which it also shows in northern Michigan, as reported by Buttrick (1923), but it apparently cannot establish itself in open places where competition by pines has been removed. This indicates need of protection by forests, perhaps to shield against late frosts. During the spring of 1940 all young shoots of Quercus standing in the open places were frost-killed. Such injury repeated at short intervals may inhibit vigorous growth; for, in the end the extremes, not the average, limit extension and establishment of vegetation types, which also agrees with the opinion expressed by Rosendahl and Butters (1928) for establishment of the maple-basswood association in Minnesota.

Reproduction by the dominant pines is not very prolific, but *Pinus strobus* has a larger number of stems in the small-size classes than *P. resinosa.* In a half-acre plot at the Point Woods *Pinus resinosa* has only one and *P. strobus* has 29 stems up to 5 inches

D.B.H. (Table 4). However, in the same area *P. resinosa* is represented with 65 stems above 10 inches D.B.H. and *P. strobus* with only one. The basal area figures accentuate the importance of a given species even more than abundance figures. Basal area (Tables 1 & 3) clearly shows the importance of *Pinus strobus* at the Dairymen's Country Club forest and *P. resinosa* in the Point Woods. In the latter stand the difference in basal area between the two species of pine is 16:1.

Adjacent to the stand on the Dairymen's Country Club property the forest has been denuded completely, and later it had no doubt also been swept by fire, for no large trees are found for a mile or more eastward. Here a dense stand of young pines has developed during the past 15 years from seeds disseminated by the mature forest to the west. The young trees are a prominent feature in a wide area otherwise almost devoid of tree growth. Two eighth-acre plots were laid off for study eastward of the mature forest, and it was found that the composition of the young stand is about the same in both plots, though the easternmost, which is removed between 200 and 350 feet from the mature stand, has fewer species participating in the association complex, and the density of the dominant species is about 10 percent less (Table 5). The youthful character of the stand is expressed by the small diameter of the trunks, by the large number of stems per unit area, and by the high percentage of dead stems (approximately 37 percent). These features are shown in Table 5. The total number of the dominant species in the one-fourth acre plot is 210, while a comparable plot in the mature forest has only 38 stems.

IN THE HARDWOOD STANDS

The stands of hardwoods considered were scattered over a wider area than the pine forests, and involved more stages of development than the pine forests. making possible observations from early youth to decadent maturity. Representatives of the typical primeval forest were the Caro Woods (Tables 6, 7, & 8): the Roach Lake stand (Tables 9 & 10); the Potzger Bog Forest (Tables 11 & 12); and the one on the Marathon Corporation property in Gogebic County, Michigan (Tables 13 & 14). Among decadent stands may be listed those on the Dairymen's Country Club property (Table 15) and the Chequamegon National Forest (Tables 18 & 19). The Forest Lake stand (Tables 16 & 17) is representative of a forest after some disturbance by cutting, and the one at Scaffold Lake (Table 20) pictures secondary succession from complete denudation of a former hardwoods.

Though the complex of species playing a part in the crown cover is not so simple as in the pine stands, it is still very simple when compared with the southern mixed hardwoods association, such as found in Indiana, where up to 40 species play a part. The most common, and always present, species are *Tsuga canadensis, Acer saccharum,* and *Betula lutea.* The only other species of tall tree which at times becomes codominant in the crown cover is *Tilia americana;* but its distribution is scattered and erratic (Tables 8-20). One exception to the general trend is found in the Chequamegon forest where *Ulmus americana* is represented by a few large stems. The percent of fidelity of the species of tall trees present in the seven stands is: *Acer saccharum,* 100; *Betula lutea,* 100; *Tsuga canadensis,* 100; *Tilia americana,* 43; *Abies balsamea,* as secondary species, 85. Though Abies shows a high fidelity, it has a low percent of frequency in all but the decadent Dairymen's Country Club hardwoods. Under the crown cover of the hardwoods there are really no shrub and small tree strata developed. The only shrub present at all regularly is Corylus. *Acer saccharum* outnumbers all other species in reproduction but its abundance in mature forests indicates very high mortality during its development. In forests where young trees over three feet in height, but under one inch in diameter, were tabulated, *Acer saccharum* had a greater representation than all other species combined. Tsuga shared this abundance in stems over 10 inches D. B. H. It is striking how abundance of stems per unit area of the dominant species (one inch or above D. B. H.) decreases with maturity (Table 22). Quercus is not a component of the hardwoods complex (Tables 6-20), but holds a subdominant position in the pine association (Tables 1-4). Two transition tendencies are obvious in the hardwoods; one, which occurs where there is increasing soil moisture, is toward the cedar-spruce or fir-spruce forest of bogs; the other, which occurs where there is decreasing soil moisture, is toward the pine association, especially toward the *Pinus strobus* variant. The hardwoods, too, consist of two variants in which one or the other of the two dominants plays a more important role. On upland sites, with decreasing soil moisture, *Acer saccharum* predominates; in the more moist lowland habitats *Tsuga canadensis* predominates (Tables 10, 12 & 14). Basal area figures in Tables 10 and 12 also show the great importance of *Betula lutea* in the forest complex in spite of its low F. I. and small abundance. Secondary succession is short; in many instances the young of the dominants occupy the soil completely from the beginning. However, in the hardwood areas fire or extreme disturbance of the crown cover favor *Acer saccharum.* This is shown at Scaffold Lake (Table 20) where Tsuga is very poorly represented, appearing not at all in the one-eighth acre plot, and where *Betula lutea* has a very insignificant representation.

In the natural establishment of seedlings of these species decaying logs seem to be of extreme importance (Table 21). Fire not only consumed these natural "seedling beds" but also deprived the shallow "A" horizon of much of its humus content. *Acer saccharum,* as shown by Gates (1917), has a potentiality for a wide range in habitat suitable to invasion and ecesis. Its prolific reproduction in the Scaffold Lake stand established competition too great

for *Betula lutea* and Tsuga. Partial cutting, not followed by fire, permits both Betula and Tsuga to reproduce in sufficient abundance to insure representation in the developing stand comparable to that in the primeval forest of the region (Tables 15 & 16). The tendency for pine and hardwoods to merge is well shown in Table 24. In certain parts scattered trees of *Pinus strobus* associate with broadleaved species, as represented by sections one to four in the transect. *Acer saccharum* crowds deep into the pine-controlled area but disappears in places where pine dominance is well expressed (sections 14 to 17). *Betula papyrifera* apparently replaces *B. lutea* in the tension zones.

THE ROLE OF DECAYING LOGS

In a primeval forest operate all factors which control mature stands in general and reproduction in particular. Usually fallen trees are thought of as playing a part only in the ever-deepening layer of soil, but a study of the stands heretofore described forced acceptance of the conclusion that fallen trees (logs) long before their reduction to humus, play a vital part in the undisturbed forest to perpetuate a specific forest complex. Table 21 presents the results of the study of decaying logs. The most outstanding single fact is that they no doubt constitute selective habitats, or oases of microclimate, in these northern hardwoods which favor Tsuga but especially *Betula lutea.* They apparently offer these two species the opportunity to compete with the extremely aggressive *Acer saccharum.* The latter species ordinarily occupies the surface soil to the exclusion of any and all other species, but for some reason cannot ecese on decaying logs. Of the 1,712 seedlings and small trees counted in the quadrats on decaying logs only 11 were *Acer saccharum.* In many instances the logs were lying in a veritable thicket of young *Acer saccharum* (Table 21). Along the border of the Potzger Bog Forest, which was free from competition by herbs and tree seedlings, *Betula lutea* seemed to reproduce well even on mineral soil. That *Betula lutea* customarily has its start on decaying logs in the forest turnover is also indicated by the peculiar clump-like distribution of the species in the mature stand. In the pine association *Pinus strobus* is apparently favored by the decaying log habitat. This also agrees with the findings by Shirley (1941).

DISCUSSION

THE PINE FORESTS

From pollen studies which have been made in widely separated geographical locations within the lake forest by Wilson and Potzger (1943) for Minnesota; Potzger (1943), Potzger and Richards (1942) for Wisconsin; Potzger and Wilson (1941), Wilson and Potzger (1943) for Michigan; Potzger and Otto (1943) for New Jersey, it has been definitely shown that Pinus occupied so prominent a place in the crown cover of forests of the past that one can consider it almost a pure stand of pine. The time during which such forest types were in control varies as one moves from upper Indiana northward. In the Vilas County, Wisconsin area moderating climate brought the simple deciduous forest, associated with Tsuga (Figs. 22-24) into the more favorable habitats and introduced the unique pine-deciduous cover types into the lake forest—a feature for which it is noted. Pinus was thus reduced to a status of relic, persisting as isolated trees in the mass of deciduous forests (Table 24), or maintaining control of the crown cover in less favorable sandy habitats as post-climax (Tables 1 & 3).

The region about Trout Lake, Vilas County, Wisconsin was and still is typical "pine country," where *Pinus strobus* and *P. resinosa* made up the greater percentage of the forest cover before cultural influences reduced all to early secondary succession, leaving in most cases not even isolated seed trees from which new pine forests might radiate. The merging tendency in nature is sufficiently well recognized to make discussion of it here necessary. In this northern part of Wisconsin it has been found that under maximum habitat requirements, *Pinus strobus* and *P. resinosa* form a somewhat balanced association, however the two species differ in their potentiality to endure certain edaphic factors, especially soil moisture. *Pinus resinosa* is more resistant to drought, and so it is found to be more prominent on sandy upland ridges and plains (Tables 3 & 4), sharing dominance with *P. strobus* in merging habitats, and yielding to the latter in moist, sandy soil (Table 1). *P. strobus* may give way to boreal forest in bogs and wet lowlands, as shown in the maps by Cunningham and White (1941) for the upper peninsula of Michigan, or be reduced to relic representation in better loam soils occupied by northern hardwoods. There is thus a mesh of interlinking forest types, each one simple in sociology, which constitute the buffer lake forest, an extremely fascinating association because of the merging tendencies. For the upper peninsula of Michigan Cunningham and White (1941) have shown the mosaic arrangement of these forest types excellently in a colored map, and Dansereau (1944) has recently described this same characteristic in the forests of Quebec. *Pinus strobus,* of all species, has the greatest potentiality to endure wide ranges of habitat factors (Tables 1, 3 & 24).

One is impressed with the length of time it required to conquer once again by stately pine the vast areas which are now covered only by low shrubs. Once upon a time not so far in the past the "Point" type of pine forest (Table 3) covered the vast sandy stretches about the Great Lakes. Lumbering and subsequent fires exterminated not only the younger growth but even the last few older trees from which disseminules might have come to build a new generation of pines. There are places, however, where such centers of distribution are present, and where new forests are springing up. Such a place is to be found along the border of the Dairymen's Country Club stand (Table 5). Advance of forests from centers of distribution are also reported by Griggs

(1934) for the edge of the forests in Alaska, where "mother trees," whose heavy, now dead, lower branches indicate their beginning as outposts in the open, are at present two miles back from the forest's edge, but are surrounded by a dense stand of younger trees. In the face of such clear indications of the natural process of forest building along unoccupied territory in the Arctic, one would think that artificial reforestation could be patterned after the natural procedure in order to assure a more rapid reclaiming for forests of the waste lands which have been lying idle for 50 to 75 years. Such procedure in reforestation work would be especially advisable since solid planting on the vast stretches seems almost prohibitive for several centuries to come. To give forests a beginning it is apparently only a matter of providing centers for germule dissemination. This may, however, be beside the point since an ecologist is primarily interested not so much in the problem of what might be done to provide forests which would be of economic value in the shortest possible time as in the discovery of natural laws operating in a vegetation complex. While time is of little significance in the progress of natural laws with man ruled out, it may become the prime factor when man forms the beginning and end of the cycle. The element of time offers a forester a different set of problems and expressions of laws from those of an ecologist. The difficulties of a forester are multiplied by the cost of reducing modifying influences, and by the selection of species with greater economic value for a given habitat, especially where the one of lesser value is favored by characteristics of important significance in competition. For him not only have time and value been added to the problem but they form the center toward which he must direct the governing laws. This is excellently shown by Shirley (1941) in his bulletin: "Restoring Conifers to Aspen Lands in the Lakes States."

An ecologist, of course, recognizes not only the natural laws which are reflected in a stand of mature forest but he is also interested in the selection and intensification of certain factors, as well as in the addition of others by the activity of man, primarily of civilized man. Denudation is usually more destructive, more general, and more persistent in the wake of man's activity than under the control of natural laws with man ruled out. Lumbering, fires, (especially repeated fires) and the protection of certain animal life beyond the balance of natural control may at times almost obscure the natural laws by which the forests of 100 years ago matured, died, and re-developed. For example, deer are perhaps more abundant now in the area discussed than they were in the days of extensive primeval forest, for, as Leopold (1943) describes, they are given a semi-domesticated animal protection. This may result, as Shirley (1941) discusses, in an almost complete destruction of beds of seedling conifers when forage is low in autumn and in winter. In the pine stand at Dairymen's Country Club all fir are severely clipped as high as deer can reach, indicating that the forest is evidently overgrazed in the winter season. While as a whole such modifying factors of the natural laws under which vegetation developed and matured are not evident in pollen profiles, widespread catastrophic destruction of forests in a given area are indicated, as shown by Potzger and Keller (1944) at the Broken Bow Lake bog. In this particular bog one foot-level recorded a sudden decline in the abundance of pine, and a decided rise in Betula, then a reversal to complete dominance by pine in the next higher foot-level. An extensive conflagration might account for such behavior of the two genera in question. While it appears unlikely to the writer that all evenaged stands of primeval forest owe their origin to a conflagration, an opinion expressed by Maissurow (1941) claims such controlling influence of fire in forest building throughout the ages.

To return, then, to our real concern. Climate is no doubt the prime selector of vegetation types. Up to the present we have, perhaps, no better record of past vegetational changes in glaciated regions than pollen profiles from lake and bog sediments. In these we find a compressed time scale and vegetational record which indicate climatic changes of the past and response of vegetation to them. In substance, Cain (1945) has recently expressed the same opinion. From these pollen records we know that pine followed spruce as undisputed climax cover (Figs. 18-24) in the part of Wisconsin under consideration here, and in turn pine yielded dominance on better loam soils to the northern hardwoods (Figs. 22-24). This competition eliminated *Pinus resinosa* and *P. banksiana* entirely from habitats constituted of better loam and clay soils, and limited *P. strobus* to scattered relic representations, of which a few colonies are still found in northern Indiana, as shown by Welch (1936). Her maps were used to indicate county distribution in Fig. 1. When this competition is removed by man, pine still finds such habitats of good soils favorable to good development in northern Wisconsin, and even in areas in Indiana now occupied by the southern deciduous forest. The climate is not entirely unfavorable to pine, as luxuriant growth in man-controlled plantings in Indiana show, and as Shirley (1941) has pointed out for the Lakes States, but it is unfavorable indirectly in that it is also favorable to the more aggressive and more tolerant broadleaved species. These broadleaved species may not be able to develop mature stands on sandy soil in the lake forest, but in some instances they offer severe competition to the conifers during the seedling stage, especially after catastrophic destruction of pine (Shirley, 1941). Pine would, indeed, reclaim the sandy areas in the region under consideration if centers of seed distribution were sufficiently abundant (Table 5). However, it would be a much slower process than reforestation by seedling plantings.

The young stand of pine adjacent to the mature forest referred to frequently (Table 5) is outstand-

ing because of the large number of stems in a unit area, and the high mortality among the competing individuals. In this 15-year old stand 37 percent of the stems are dead. The mortality runs higher if all competing species are considered. Elimination of individual trees will no doubt continue, as is indicated by the fact that in the mature stand, a few feet to the west, were found only 19 stems in a one-eighth acre plot, and in the Point Woods only 17 stems to a like area. In two similar plots in the young stand we recorded 98 and 112 stems, respectively. Mortality seems to be higher among *Pinus strobus* than among *P. resinosa*—at least in the stems ranging between one and four inches D. B. H. (Table 5).

The open crown of the pines is reflected in a rather rich ground cover of herbs and seedlings of trees (Table 23). Of the 39 species present in the herbaceous layer, 14 were woody plants; seedlings of the dominants in the arboreal layer were poorly represented, accentuating a decided intolerance of these conifers. It is, therefore, very evident that tolerant broadleaved species could easily crowd out the pines if climate were favorable to their invasion. This is so graphically expressed in all pollen profiles of Indiana and southern Michigan (Figs. 6-11).

Though the numbers of species appearing in the above-mentioned ground cover study is large, frequency is low for most of them. This is, however, what one would expect according to Raunkiaer's law of frequency. *Acer rubrum* (F. I. 95) is the most widely distributed species in the ground cover, agreeing with its importance in the large-stem classes of the mature pine forest (Tables 1, 2). The most abundant, and most universally distributed herbaceous species is *Maianthemum canadense,* with *Trientalis borealis* (F. I. 80) a close competitor. The bracken fern plays a very important role in the ground cover because of shading by the wide fronds. One of the most significant factors accentuated by Table 23 is the apparent inability of the conifers to reproduce well under the crown cover of the parent association, evidently requiring more light than many of the herbs and a few of the broadleaved tree species require. The high frequency and great abundance of *Acer rubrum* and *A. saccharum* (Table 23) compared with their decided lesser importance in the larger stem classes (Tables 1 & 3) reflect the secondary position of these species in the mature pine stand. One would, however, expect that the species offer a tremendous competition to seedlings of the pines. This agrees with the findings of Smith (1940) in cutover stands of *Pinus strobus* in central New England, and with Shirley (1941), who reports the same competition for pine seedlings by aspen and bracken fern.

THE HARDWOOD STANDS

In the study of the northern hardwood stands the pollen profiles, again, present the most reliable data on their position in climatic succession, and upon the status of the broadleaved forest today (Figs. 12-14; 22-24). Climatically it has been favored most recently, for it followed in succession a very decided dominance by Pinus. However, it is limited in extent by edaphic factors, as indicated by a comparison of Figs. 18-21 with 22-24. As stated before, the sociology of the northern hardwoods is more simple than that of the pine forests when secondary woody species are taken into account; the former has one-half, or even less than half, as many woody species as the latter. The crown canopy is controlled in most instances by three species, *Acer saccharum, Betula lutea* and *Tsuga canadensis,* with the addition of *Tilia americana* in some localities. The former three species show a fidelity of 100 percent in the stands studied; these stands represent at least 75 miles of geographical distribution in north central Wisconsin (Fig. 1). *Acer saccharum* shows the same potentiality of invading habitats with reduced soil moisture as it exhibits in Indiana in the tension zones between mixed hardwoods and Quercus-Carya. In Indiana it persists to the very ridge-tops of north-facing slopes, and frequently invades the drier south-facing slopes (Potzger, 135, 1939; Potzger and Friesner, 1940). In the stands studied in Wisconsin, *Acer saccharum* increases in abundance on the well-drained uplands and slopes, and *Tsuga canadensis* shows a compensating reduction in representation; the process is reversed in the less drained lowlands. *Betula lutea* is apparently very little influenced by the small relief in the forests studied (Tables 10, 12 & 14). Acer has without doubt the advantage in secondary succession when former vegetation is destroyed completely as it has been at Scaffold Lake (Table 20). However, this might be entirely different if the microclimate of decaying logs remained after destruction of the crown cover. Limited as the present observations on decaying logs have been (Table 21), there seems to be no doubt that such logs are a vital factor in the perpetuation of the unique three-species association in the hardwoods of this part of Wisconsin and Michigan. The writer feels even more keenly now than he had felt before that it is a mistake to "clean up" a forest and at the same time expect continuation of a natural development. Whether it is moisture, acidity, or some other factor which causes the selection of Betula and Tsuga by decaying logs, and the almost complete elimination of *Acer saccharum,* cannot be determined by the results of the present survey. The problem is, however, worthy of further study.

SUMMARY AND CONCLUSIONS TO PART I

1. Part I presents data on a phytosociological survey of two stands of pine and 8 stands of northern hardwoods in Price and Vilas Counties, Wisconsin, and Gogebic County, Michigan, in which frequency index, density, fidelity, coverage, and basal area are considered. The sampling unit was 100 square meters.

2. *Pinus strobus* and *P. resinosa* association finds expression in two forest variants according to abundance of one or the other of the two species. The *Pinus resinosa* variant occupies drier upland sites.

3. Crown coverage in the pine stands is low,

which permits development of a fairly well expressed herbaceous layer. A second layer tree stratum consisted primarily of *Quercus borealis* var. *maxima, Acer rubrum,* and *A. saccharum.* The broadleaved representatives in the stand are apparently unable to participate in the crown cover.

4. Reproduction by the dominant pines is very poor under the forest canopy, but it is very prolific in open habitats adjacent to the mature stand. Acer and Quercus do not participate in the sociological complex of a stand of young pines.

5. Of the 8 stands of northern hardwoods considered only 5 were comparatively undisturbed. The disturbed stands were included to show successional tendencies.

6. Northern hardwoods are expressed as two variants, determined by greater abundance of either *Acer saccharum* or *Tsuga canadensis,* where Acer represents habitats with less soil moisture.

7. Crown coverage is 90 to 100 percent in the hardwoods, so the herbaceous layer is wanting.

8. Species showing highest fidelity, abundance, and frequency are *Acer saccharum, Tsuga canadensis,* and *Betula lutea.*

TABLE 1. Tabulation from fifty 10-meter quadrats in the pine stand on Dairymen's Country Club Property, Vilas County, Wisconsin.

Species	Number of stems in six diameter classes (inches)						Total	F.I. (*Per-cent*)	Basal area in sq. ft.
	Below 1 in.	1–5	6–10	11–15	16–20	Above 20			
Abies balsamea	97	205	2				304	74	3.0
Acer rubrum	57	103	7				167	74	4.2
Acer saccharum	10	71	11				92	60	6.0
Amelanchier sp.	2	3	1				6	10	.1
Betula papyrifera	2	21	3		1		27	16	1.6
Corylus cornuta	101						101	44	
Pinus resinosa	1	1	5	21	41	9	78	70	116.9
Pinus strobus	10	5	20	38	42	18	133	94	167.5
Prunus pennsylvanica		1					1	2	.02
Prunus virginiana	4	14					18	16	.3
Quercus borealis var. *maxima*	1	4	3				8	12	1.3
Tsuga canadensis		1	1				2	4	.8

TABLE 2. Tabulation of one-half acre plot in pine stand on Dairymen's Country Club Property.

Species	Number of stems in seven diameter classes (inches)							Total above 1 in.	Basal area in sq. ft.
	Below 1 in.	1 in.	2–5	6–10	11–15	16–20	Above 20		
Abies balsamea	55	75	83					158	2.7
Acer rubrum		35	53	1				89	2.7
Acer saccharum		25	39	2				66	2.4
Amelanchier sp.		1						1	.1
Betula papyrifera		1		1	5			7	4.5
Pinus resinosa				1	4	9	3	17	25.0
Pinus strobus	1			14	16	22	6	58	76.6
Prunus virginiana	8							8	.4
Quercus borealis var. *maxima*			2					2	.1
Tsuga canadensis				2				2	.7

TABLE 3. Tabulation from twenty 10-meter-square quadrats in Point Norway pine stand, Vilas County, Wisconsin.

Species	Number of stems in seven diameter classes (inches)							Total stems	F.I. (*Per-cent*)	Basal area in sq. ft.
	Below 1 in.	1 in.	2–5	6–10	11–15	16–20	Above 20			
Abies balsamea	18	3	2	1				24	35	0.3
Acer rubrum	36	17	37	4				94	90	2.6
Acer saccharum	62	42	53	4				161	60	3.5
Acer spicatum	1							1	5	
Alnus incana	1							1	5	
Amelanchier sp.	18	12	3					33	60	.1
Betula lutea			1					1	5	.1
Betula papyrifera		3	8	2				13	25	1.4
Corylus cornuta	374							374	90	
Lonicera sp.	17							17	30	
Nemopanthus mucronata	1							1	5	
Picea glauca		1						1	5	
Pinus resinosa		2	3	4	42	28	9	88	100	117.5
Pinus strobus		11	32	4	4	2		53	60	11.1
Quercus borealis var. *maxima*	6	9	27					42	55	1.0
Thuja occidentalis			1					1	5	.08

TABLE 4. Tabulation of stems 1-inch or above in diameter on one-half acre in the Point Woods.

Species	Number of stems in seven diameter classes (inches)							Total above 1 in.	Basal area in sq. ft.
	Below 1 in.	1 in.	2–5	6–10	11–15	16–20	Above 20		
Abies balsamea	5		1					1	0.02
Acer rubrum		14	26	1				41	1.3
Acer saccharum		21	28	2	3			54	5.5
Amelanchier sp.		22	11					33	.5
Betula papyrifera		1	11	1				13	1.0
Picea glauca	15								
Pinus resinosa	1			1	21	39	5	63	97.7
Pinus strobus		5	25	3	1			34	3.3
Prunus virginiana		2						2	.01
Quercus borealis var. *maxima*		9	38					47	2.0

TABLE 5. Tabulations of living and dead stems in two one-eighth acre plots of young pine stands east of the mature forest on Dairymen's Club Property. (A) adjoining mature forest. (B) adjoining (A) to the east.

Species	Living Stems									Basal area in sq. ft.	Dead Stems					
	Below 1 in.	1	2	3	4	5	6	7	Total		Below 1 in.	1	2	3	4	Total
(A)																
Abies balsamea	2		1	4	1	7	1	2	18	2.1		3	2	1	2	8
Acer rubrum		1	1	1		1			4	.2	2	2	1			5
Pinus resinosa			1			1	2		4	.6						
Pinus strobus	4	19	25	34	15	8	2	1	108	5.5	17	9	9	4	2	41
Prunus virginiana			1						1	.02		2				2
Tsuga canadensis		1							1		1					1
Betula papyrifera			1	4					5	.2						
(B)																
Abies balsamea					1				1	.09	5	3	2			10
Acer rubrum											5	1				6
Pinus resinosa		1		2	3	6	2	2	16	2.1	1	1			1	3
Pinus strobus	7	21	19	16	13	4	2		82	3.4	27	18	6	3		54

TABLE 6. Summary of twenty-five 10-meter-square quadrats tallied in hardwoods at Pike Lake, Price County, Wisconsin. (Caro Woods.)

Species	Number of stems in six diameter classes (inches)						Total stems	F.I. (*Percent*)	Basal area in sq. ft.
	Below 1 in.	1–5	6–10	11–15	16–20	Above 20			
Abies balsamea		2					2	8	
Acer saccharum	225	10	3	5	4	2	249	68	19.4
Acer spicatum	11						11	16	
Betula lutea		1	1	1	7	7	17	52	34.2
Dirca palustris	1						1	4	
Fraxinus sp.	3						3	8	
Thuja occidentalis			1				1	4	.3
Tilia americana	1				2	6	9	28	22.9
Tsuga canadensis		17	39	32	19	10	117	96	109.6

TABLE 7. Tabulation from one-half acre of woody plants in Caro Woods, near Pike Lake, Price County, Wisconsin.

Species	Number of stems in seven diameter classes (inches)							Total stems 1 in. or above	Basal area in sq. ft.
	Below 1 in.	1 in.	2–5	6–10	11–15	16–20	Above 20		
Acer saccharum	37	3		6	1			10	3.0
Acer spicatum	28								
Betula lutea			1	1	3	3	9	17	38.3
Tilia americana	1	1	2			1	2	6	6.6
Tsuga canadensis		2	11	29	19	15	1	77	55.8

NOTE: Foresters have given age of following trees in the Caro Woods with diameters stated below as: Tsuga, 16.5 in. D.B.H., 215 years; Tilia, 29.0 in. D.B.H., 380 years; Betula, 16.0 in. D.B.H., 210 years.

TABLE 8. Tabulations from two one-eighth acre plots in Caro Woods, showing variants of hardwoods. (A) Lowland. (B) Ridge.

Species	Number of stems in seven diameter classes (inches)							Total above 1 in.	Basal area in sq. ft.
	Below 1 in.	1 in.	2–5	6–10	11–15	16–20	Above 20		
(A)									
Acer saccharum				1	2		1	4	6.8
Betula lutea				1		3	2	6	11.5
Thuja occidentalis				1				1	.3
Tilia americana						1	1	2	4.6
Tsuga canadensis			5	13	4	1		23	9.8
(B)									
Abies balsamea	1								
Acer saccharum	27	13	1			1		15	1.5
Acer spicatum	7								
Betula lutea			1		1	3	1	6	9.0
Prunus virginiana	1								
Tsuga canadensis			3	5	5	3		16	12.2

TABLE 9. Tabulation from twenty-five 10-meter-square quadrats in hardwoods on Gillen Nature Reserve, Vilas County, Wisconsin, between Roach and Tenderfoot Lakes.

Species	Number of stems in six diameter classes (inches)						Total stems	F.I. (*Percent*)	Basal area in sq. ft.
	Below 1 in.	1–5	6–10	11–15	16–20	Above 20			
Abies balsamea		5					5	16	0.1
Acer saccharum		20	4	6	12	7	49	84	50.3
Acer spicatum		4					4	8	.04
Betula lutea		3	5	6	6	7	27	76	44.8
Ostrya virginiana		5	1				6	12	.07
Thuja occidentalis		3	3	1			7	24	2.4
Tilia americana		4	5			1	10	24	5.7
Tsuga canadensis		34	51	19	7	11	122	92	81.5

TABLE 10. Tabulation from four one-eighth acre plots in hardwoods on Gillen Nature Reserve, near Roach Lake, Vilas County, Wisconsin, showing variants in the stand. A, B: moist lowland; C, D: drier ridges.

Species	Number of stems in six diameter classes (inches)						Total stems	Basal area in sq. ft.
	1 in.	2–5	6–10	11–15	16–20	Above 20		
(A)								
Abies balsamea	1	2	1				4	0.4
Acer saccharum	2	3					5	.1
Betula lutea			2	1	3	2	8	12.9
Tsuga canadensis		5	11	6	3	2	27	21.3
(B)								
Acer saccharum				2		1	3	5.0
Betula lutea			2		3	2	7	12.2
Tsuga canadensis		5	14	7	1	1	28	15.6
(C)								
Abies balsamea		1					1	.09
Acer saccharum	4	5		2	1	2	14	9.4
Betula lutea			4		2		6	4.9
Fraxinus americana		1					1	.1
Ostrya virginiana		1	1				2	.2
Tilia americana		3	4	1	1		9	3.7
Tsuga canadensis	1	4	2	2			9	2.6
(D)								
Acer saccharum		6	2	4	1	1	14	9.9
Betula lutea			3	1	1		5	3.7
Tilia americana	1	4		1	2		8	8.3
Tsuga canadensis		7	3		1		11	3.5

TABLE 11. Tabulation from ten 10-meter-square quadrats in hardwoods on Gillen Nature Reserve, above Potzger Bog, Vilas County, Wisconsin.

Species	Number of stems in seven diameter classes (inches)							Total stems	F.I. (*Percent*)	Basal area in sq. ft.
	Below 1 in.	1 in.	2–5	6–10	11–15	16–20	Above 20			
Abies balsamea		3		1				4	20	0.5
Acer saccharum	7	16	29	8	2	4		59	90	11.2
Betula lutea				6	3	7	4	20	90	30.5
Thuja occidentalis		1						1	10	
Tilia americana					3	2		5	30	6.7
Tsuga canadensis		5	47	19	2	1	2	76	100	17.8

TABLE 12. Tabulations from two one-eighth acre plots in hardwoods in Gillen Nature Reserve at Potzger Bog, Vilas County, Wisconsin. (A) near the bog; (B) upland.

Species	Number of stems in six diameter classes (inches)						Total stems	Basal area in sq. ft.
	Below 1 in.	1–5	6–10	11–15	16–20	Above 20		
(A)								
Acer saccharum			3	2			5	2.7
Betula lutea			1		2	1	4	6.4
Thuja occidentalis			1				1	.2
Tilia americana			1	1	1		3	3.2
Tsuga canadensis		27	26	2	1	3	59	21.9
(B)								
Acer saccharum		16	6	3	1		26	6.2
Betula lutea				2	1	1	4	6.2
Tilia americana			1		3		4	4.9
Tsuga canadensis		4	3	1			8	1.6

TABLE 13. Tabulation from twenty-five 10-meter-square quadrats in Marathon Corporation Forest, one-half mile south of Highway No. 2.

Species	Number of stems in seven diameter classes (inches)							Total above 1 in.	F.I. (*Percent*)	Basal area in sq. ft.
	Below 1 in.	1 in.	2–5	6–10	11–15	16–20	Above 20			
Abies balsamea		2	1	1				4	8	0.3
Acer rubrum			1					1	4	.1
Acer saccharum	?	25	22	11	14	8	7	87	84	55.9
Acer spicatum	17								8	
Betula lutea		1	2	6	5	3	12	29	72	58.9
Corylus sp.	76									
Dirca palustris	4									
Tsuga canadensis			11	21	20	7	2	61	80	45.5

TABLE 14. Tabulation from four one-eighth acre plots in hardwoods in Marathon Corporation Forest, Gogebic County, Michigan, showing variants. A and B: Upland; C and D: Lowland.

Species		Number of stems in six diameter classes (inches)						Total stems	Basal area in sq. ft.
		1 in.	2–5	6–10	11–15	16–20	Above 20		
Abies balsamea	A	..	..	..	..	..	..	..	....
	B	..	1	1	..	..	..	2	0.3
	C	..	3	..	..	..	..	3	.06
	D	..	1	..	..	..	..	1	....
Acer saccharum	A	5	9	3	1	2	3	23	17.1
	B	9	3	5	1	2	1	21	9.9
	C	3	3	2	6	1	1	16	10.2
	D	5	3	1	1	..	..	10	2.0
Acer spicatum	A	..	..	..	..	..	..	..	....
	B	..	..	..	..	..	..	..	....
	C	2	..	..	..	..	..	2	....
	D	2	..	..	..	..	..	2	....
Acer rubrum	A	..	..	..	..	..	..	..	....
	B	..	..	..	..	..	..	..	....
	C	..	1	..	..	..	..	1	....
	D	2	2	1	..	..	..	5	.3
Betula lutea	A	..	..	1	..	..	1	2	3.0
	B	..	..	..	..	1	2	3	11.5
	C	1	1	2	1	..	1	6	5.4
	D	..	..	..	..	1	4	5	14.0
Corylus	A	..	..	..	..	..	..	..	....
	B	..	..	..	..	..	..	..	....
	C	(2)	..	..	..	..	..	..	....
	D	..	..	..	..	..	..	..	....
Picea glauca	A	..	..	..	..	..	..	..	....
	B	..	..	..	..	..	..	..	....
	C	..	..	..	..	..	..	..	....
	D	1	..	..	..	..	..	1	....
Thuja occidentalis	A	..	..	..	..	..	..	..	....
	B	..	..	..	..	..	..	..	....
	C	..	..	..	..	..	..	..	....
	D	..	..	..	1	..	..	1	.8
Tsuga canadensis	A	..	1	3	1	..	..	5	1.7
	B	..	..	2	3	3	..	8	8.3
	C	..	2	5	2	2	..	11	6.5
	D	..	2	1	1	2	3	9	13.5

TABLE 15. Tabulation from twenty 10-meter-square quadrats in hardwoods on Dairymen's Club Property, Vilas County, Wisconsin.

Species	Number of stems in seven diameter classes (inches)							Total stems	F.I. (*Percent*)	Basal area in sq. ft.
	Below 1 in.	1 in.	2–5	6–10	11–15	16–20	Above 20			
Abies balsamea	38	11	22	...	...	...	...	71	70	1.1
Acer rubrum	5	4	1	1	2	...	...	13	35	2.2
Acer saccharum	17	17	26	27	2	...	...	89	80	14.6
Betula lutea	...	...	1	3	4	3	1	12	45	18.1
Betula papyrifera	...	...	4	8	8	1	1	22	45	11.0
Ostrya virginiana	...	...	3	...	...	...	...	3	15	.2
Pinus strobus	...	...	...	...	2	2	1	5	15	7.4
Tsuga canadensis	...	10	30	14	11	3	3	67	85	30.8

TABLE 16. Tabulation from twenty-five 10-meter-square quadrats in hardwoods north of Forest Lake, Vilas County, Wisconsin.

Species	Number of stems in seven diameter classes (inches)							Total stems	F.I. (*Percent*)	Basal area in sq. ft.
	Below 1 in.	1 in.	2–5	6–10	11–15	16–20	Above 20			
Abies balsamea	...	10	5	3	...	...	...	18	40	1.5
Acer saccharum	32	16	53	23	15	3	3	145	92	29.6
Betula lutea	...	1	2	11	11	7	1	33	72	29.9
Betula papyrifera	...	...	...	2	4	3	1	10	36	9.7
Corylus cornuta	2	...	...	...	...	...	...	2	8	...
Pinus strobus	...	...	...	...	...	1	1	2	8	5.2
Tsuga canadensis	...	5	49	80	17	2	...	153	100	4.7

TABLE 17. Tabulation of stems one inch or above D.B.H. from one-eighth acre in hardwoods near Forest Lake, Vilas County, Wisconsin.

Species	Number of stems in seven diameter classes (inches)							Total stems	Basal area in sq. ft.
	Below 1 in.	1 in.	2–5	6–10	11–15	16–20	Above 20		
Abies balsamea	...	1	1	...	...	...	...	2	.2
Acer saccharum	...	...	1	2	4	...	...	7	4.0
Betula lutea	...	...	...	...	3	1	...	4	4.3
Betula papyrifera	...	...	...	1	2	...	...	3	2.1
Tsuga canadensis	...	1	19	17	3	...	...	40	10.4

TABLE 18. Tabulation from twenty 10-meter-square quadrats in hardwood stand in Chequamegon National Forest near head of Willow Creek, Price County, Wisconsin.

Species	Number of stems in seven diameter classes (inches)							Total stems	F.I. (*Percent*)	Basal area in sq. ft.
	Below 1 in.	1 in.	2–5	6–10	11–15	16–20	Above 20			
Acer saccharum	388	33	60	5	11	6	5	508	95	40.0
Betula lutea	..	...	...	1	...	3	2	6	20	13.5
Corylus sp.	33	...	...	...	...	...	...	33	25	...
Fraxinus americana	12	...	1	...	...	...	...	13	35	.05
Ostrya virginiana	46	5	25	4	...	...	...	80	75	2.6
Tilia americana	14	3	5	1	1	1	4	29	50	25.1
Tsuga canadensis	...	...	2	8	5	6	4	25	70	29.8
Ulmus americana	1	...	...	...	...	2	...	3	15	7.6
Quercus sp.	3	...	...	...	...	...	...	3	10	...
Dirca palustris	1	...	...	...	...	...	...	1	5	...

TABLE 19. Tabulation of woody plants from one-eighth acre in Chequamegon National Forest, Price County, Wisconsin.

Species	Number of stems in seven diameter classes (inches)							Total stems	Basal area in sq. ft.
	Below 1 in.	1 in.	2–5	6–10	11–15	16–20	Above 20		
Acer saccharum	...	14	10	...	1	1	2	28	9.6
Betula lutea	...	...	...	1	...	2	1	4	8.9
Ostrya virginiana	...	...	7	...	...	...	...	7	.5
Tilia americana	...	1	1	...	...	...	1	3	3.0
Tsuga canadensis	...	...	1	1	...	...	1	3	1.3

TABLE 20. Tabulation of woody plants in one-eighth acre in hardwoods above Scaffold Lake, Vilas County, Wisconsin. D.B.H. in inches.

Species	Below 1 in.	1	2	3	4	5	6	7	8	9	10	11	Total stems	Basal area in sq. ft.
Acer rubrum	..	1	6	6	4	...	...	...	...	...	...	...	17	.7
Acer saccharum	38	81	49	36	10	2	...	...	...	...	...	1	217	8.8
Betula lutea	..	...	1	...	...	...	...	...	...	...	...	...	1	.05
Betula papyrifera	..	...	...	1	1	1	...	...	...	...	...	...	3	.3
Ostrya virginiana	1	1	8	6	3	2	...	...	...	...	...	...	21	1.0
Populus tremuloides	..	...	1	...	1	1	1	...	1	1	...	...	6	1.2
Prunus virginiana	..	...	1	1	...	...	...	...	...	...	...	...	2	.07
Quercus borealis var. *maxima*	..	...	...	2	...	...	...	...	...	...	...	...	2	.1
Tilia americana	..	...	6	8	4	3	1	1	...	...	...	...	23	1.0

Table 21. Species of trees reproducing on decaying logs and abundance of seedlings in a strip 36 inches long by width of the log.

Location	Logs	Species represented by the log	Degree of decay	Size 36 X	*Betula lutea*	*Tsuga canadensis*	*Acer rubrum*	*Acer saccharum*	*Betula papyrifera*	*Pinus strobus*	*Pinus resinosa*	X indicates *Acer saccharum* young trees abundant (soil)
	1	Betula	Just beginning	12	26	1	..	..	..	..	..	x
	2	Tsuga	Well decayed	14	53	1	..	..	..	..	..	..
	3	Tsuga	Well decayed	15	22	..	..	..	..	..	..	x
	4	Betula	Just beginning	14	26	2	..	1	..	..	..	x
Near Forest	5	Tsuga	Well decayed	15	56	4	..	..	..	..	..	x
Lake	6	Tsuga	Well decayed	7	12	..	..	..	..	..	..	x
	7	Tsuga	Well decayed	10	36	3	..	..	..	..	..	x
	8	Tsuga	Medium	11	24	3	..	..	..	..	..	x
	9	Tsuga	Medium	6	14	..	..	..	..	..	..	x
	10	Tsuga	Just beginning	18	35	5	..	..	..	..	..	x
Total.........................4392 sq. in.					304	19	..	1	..	..	..	..
	1	Betula	Well decayed	16	13	..	6	..	..	..	..	x
	2	Tsuga	Medium	23	16	3	1	1	..	..	..	x
Marathon	3	Tsuga	Medium	17	38	5	2	..	..	..	..	..
Corporation	4	Tsuga	Medium	16	18	2	1	1	..	..	..	x
Gogebic	5	Tsuga	Just beginning	21	69	9	1	1	..	..	..	x
County,	6	Tsuga	Well decayed	16	39	4	2	2	..	..	..	x
Michigan	7	Abies	Just beginning	8	16	5	..	..	..	..	..	None
	8	Tsuga	Well decayed	10	90	8	1	..	..	..	..	Few
	9	Tsuga	Just beginning	14	19	4	..	..	..	..	..	..
	10	Tsuga	Medium	15	43	8	1	..	..	..	..	x
Total.........................5616 sq. in.					361	48	15	5	..	..	..	..
	1	....	....	12	11	1	..	..	..	..	..	..
	2	....	....	18	6	3	..	..	..	..	..	..
	3	Tsuga	....	28	8	2	..	..	..	..	..	..
Gillen Nature	4	Tsuga	....	11	96	..	..	..	..	..	..	..
Reserve near	5	Tsuga	....	16	69	15	1	..	..	..	..	..
Potzger Bog	6	Tsuga	....	12	8	..	..	..	..	..	..	..
	7	Betula	Medium	17	24	4	..	..	..	..	..	..
	8	Tsuga	Just beginning	12	13	..	..	..	..	..	..	..
	9	Tsuga	In dense moss on bark	22	124	5	1	..	..	..	..	..
	10	Tilia	Well decayed to center	16	46	3	..	..	..	..	..	..
Total.........................5904 sq. in.					405	33	..	..	..	..	..	..
	1	?	Well decayed	24	12	..	..	..	..	..	..	..
	2	?	Just beginning	10	26	3	..	..	..	..	..	..
	3	....	Just beginning	8	32	8	..	..	..	..	..	..
	4	?	Just beginning	10	39	3	..	..	..	..	..	x
Caro Woods,	5	Betula	Well decayed	6	35	..	..	..	..	..	..	x
Price County	6	Tilia	Well decayed	9	69	..	..	..	..	..	..	x
	7	?	Just beginning	10	24	7	..	..	..	..	..	x
	8	Acer	Medium	12	45	2	..	..	..	..	..	x
	9	?	....	16	55	5	..	..	..	..	..	Some
	10	Tsuga	Medium	12	33	7	..	..	..	..	..	x
Total.........................4212 sq. in.					370	35	..	..	..	..	..	..
Dairymen's	1	Betula	Well decayed	12	9	8	4	..	..	..	..	..
Country Club	2	?	Medium	12	8	11	6	..	..	..	..	..
Hardwoods	3	....	Well decayed	14	..	4	2	..	..	..	..	..
	4	....	Well decayed	10	..	2	1	5	..	..	..	..
	5	....	Well decayed	12	42	4	1	..	..	1	..	..
Total.........................2160 sq. in.					59	29	14	5	..	1	..	..
	1	?	Well decayed	11	..	..	..	..	14	..	..	..
	2	....	Well decayed	22	..	..	7	..	..	1	..	..
	3	....	Well decayed	10	..	..	8	..	3	2	..	..
Pine woods	4	....	Well decayed	9	..	..	4	..	4	2	..	..
Dairymen's	5	....	Well decayed	11	..	2	1	..	5	2	..	..
Country Club	6	....	Well decayed	9	..	..	1	..	4	..	..	..
	7	....	Well decayed	14	..	3	..	..	14	..	1	..
	8	Betula	Well decayed	12	..	1	..	..	3	..	..	..
	9	?	Well decayed	18	..	..	1	..	..	3	..	..
	10	....	Medium	10	..	..	2	..	1	3	..	..
Total.........................4536 sq. in.					..	6	24	..	48	13	1	..

TABLE 23. Tabulation of the herbaceous and seedlings of woody plant layer from twenty one-meter-square quadrats in the pine stand at Dairymen's Country Club.

Species	Density	F.I.
		Percent
Abies balsamea	3	10
Acer rubrum	118	95
A. saccharum	126	55
Aralia nudicaulis	9	25
Aster sp.	3	10
A. macrophyllus	3	15
A. Shortii	13	10
Betula sp.	26	25
Carex sp.	?	30
Corylus sp.	4	15
Clintonia borealis	30	35
Cornus canadensis	25	15
Diervilla lonicera	5	15
Epigaea repens	7	5
Galium triflorum	57	15
Grass?	13	15
Gaultheria procumbens	14	10
Lycopodium clavatum	3	5
Linnaea borealis var. *americana*	20	10
Lonicera sp.	12	10
Lactuca sp.	1	5
Maianthemum canadensis	707	95
Moneses uniflora	6	10
Oryzopsis asperifolia	24	50
Pteridium aquilinum var. *latiusculum*	81	75
Pyrola sp.	29	25
Prunus virginiana	3	10
Pinus strobus	4	15
Quercus borealis var. *maxima*	1	5
Rubus pubescens	10	5
R. idaeus	5	10
Schizachne purpurascens	1	5
Smilacina stellata	7	20
Trientalis borealis	156	80
Tsuga canadensis	2	10
Viola sp.	6	15
Viola sp.	4	5
Vaccinium canadensis	4	10
Waldsteinia fragarioides	304	65

TABLE 22. Number of stems per acre (computed) one inch or above D.B.H. in stands varying in age, disturbance, and decadence.

Stands	Characteristics	Area tabulated	Number of stems 1 in. or above D.B.H.	Stems per acre
Caro Woods, Price County	mature	1/8 acre	36	288
Gillen Nature Reserve, Roach Lake	mature	1/8 acre	38	304
Gillen Nature Reserve above Potzger Bog	mature	1/8 acre	42	336
Dairymen's Country Club pine woods	mature	1/2 acre	408	816
Point woods, pine	early maturity	1/2 acre	291	582
Chequamegon National Forest, Price County	decadent	1/8 acre	45	360
Marathon Corporation Gogebic County, Michigan	mature	1/8 acre	34	272
Forest lake stand	disturbed part cutting	1/8 acre	56	448
Scaffold Lake	early succession from bare area	1/8 acre	292	2,336
Stand of 15-year pine (1st)	developing from seedling, bare area	1/8 acre	136	1,088

TABLE 24. A 170-meter line transect from hardwoods to pine at Dairymen's Country Club property to show transitional tendencies. Each section is 10-meters-square. Figures show D.B.H. of trees, ( ) trees below 1 inch D.B.H.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Abies balsamea	2	1	.....	1–3	1–2	2 (3)	..... (2)	3	4	.....	.....	3–4 (2)	1	.....	.....	.....	.....
Acer rubrum	.....	.....	.....	.....	.....	.....	.....	..... (2)	.....	.....	2	1	1	.....	7–5	.....	.....
Acer saccharum	1–5 5	6–8 3–2 9–4	5–5 2–1	9–4	2–2 3	5–7 7	9–1 2	1–8 2–9 8–9 1–1 (1)	2–7 1–1 7	3	5	1–3 6	7–3 5	.....	.....	.....	.....
Betula papyrifera	14	17–9 15	10 24	10	16	.....	.....	.....	14–2	11	15	.....	.....	13	.....	.....	8
Corylus cornuta	.....	.....	.....	.....	.....	.....	(11)	(3)	.....	.....	.....	(1)	.....	.....	.....	.....	.....
Pinus resinosa	.....	.....	.....	.....	9	18 26	11	18	.....	12 17	17	.....	.....	15 14 12	14 20	21	20
Pinus strobus	12	8	.....	24	13–9	12–19 14 10 8–19	11 16	20 18 7	18	18 13 18 12	14 12	10 10	22–7 15 14 10 14	11 10 23	17 12	9–10 13 10 11	11 8
Prunus virginiana	.....	.....	.....	.....	.....	.....	.....	1–1	.....	.....	.....	.....	.....	.....	.....	.....	.....
Quercus borealis var. *maxima*	.....	.....	.....	.....	.....	.....	.....	(2)	.....	.....	.....	.....	.....	.....	.....	.....	.....
Tsuga canadensis	6 14	8 7	.....	9	.....	.....	.....	4	.....	10 [illegible]	7	.....	.....	.....	.....	.....	.....

TABLE 25. Forest composition expressed in terms of the percentage of the total tree population which each species showed in the smaller or larger stands of climax forest studied. For graphic representation of these percentages (averaged for a given region) see Figure 31.

Acer saccharum	*Betula lutea*	*Fagus grandifolia*	*Tilia americana*	*Tsuga canadensis*	*Ulmus* spp.	*Abies balsamea*	*Acer rubrum*	*Castanea dentata*	*Carya* spp.	*Fraxinus* spp.	*Ostrya virginiana*	*Picea glauca*	*Picea rubra*	*Pinus strobus*	*Prunus serotina*	*Quercus alba*	*Quercus borealis* var. *maxima*	*Quercus macrocarpa*	*Thuja occidentalis*	State	County or location	Author
12.0		55.0	7.0					6.0									6.0			New England		Lutz, 1928
8.9	19.0	26.1		8.5									27.3	0.5						New York		McCarthy & Belyea, 1920
40.0	8.0	36.0		6.0						2.0					2.0					New York	Alleghany Park	Taylor, 1928
13.1	6.1	30.8	3.1	26.8				5.5						6.0						Nw. Pennsylvania	Geological survey notes on 174,000 acres	Sam Dale (Lutz, 1930)
	.1	24.0		36.0										11.0		1.6	1.8			Pennsylvania	Hearts Content	Lutz, 1930
91.0	4.0		1.0		4.0															Lower Michigan	Antrim	Gleason, 1924
75.0	1.0	1.0	4.0	1.0	18.0																Otsego	"
75.0	4.0	5.0	1.0	5.0	9.0						1.0										Otsego	"
48.0		28.0	1.0	3.0	20.0																Charlevoix	"
67.0		17.0	.5	11.1	3.0		(Giv	en a	s sq.	ft. p	er ac	re,tr	ansl	ated	into	perc	ent)				Kalkaska	"
36.8	3.6	14.7	4.3	7.4	4.2												0.3			N. half Lower & E. half Upper Michigan	Part of 2,600-acre tally by U. S. Forest Service	Cunningham, 1941
				1.8																Lower Michigan	Kalkaska	McIntyre, 1931
				12.8																	Kalkaska	"
				57.8																	Kalkaska	"
				3.1																E. Upper Mich.	Luce	"
78.4	9.2	6.6																			Luce	"
23.7	4.0	17.0																			Luce	"
31.7	21.9	35.7					Give	n as	sq. f	t. pe	r acr	e, tr	ansl	ated	into	per	cent				Luce	"
59.4	4.7																				Chippewa	"
66.6																					Chippewa	"
27.6	1.1		3.3		2.7					3.0										W. Upper Mich.	Menominee	"
75.8	.5		10.9	1.4	1.4	1.6					4.9	.4			3.4				0.3		Menominee	Westveld, 1933
63.8	7.1		10.1	5.4	2.7	6.2					3.9										Menominee	"
				63.9																	Menominee	McIntyre, 1933
				14.0																	Alger	"
				1.7																W. Upper Mich.	Alger	McIntyre, 1931
				5.6																	Alger	"
				14.0																	Alger	"
				58.2																	Alger	"
				9.3																	Menominee	"
				64.3																	Menominee	"
				63.9																	Menominee	"
				72.3																	Menominee	"
34.0	22.0			47.7																	Gogebic	Potzger (Tables 6-7)
74.1	6.7	18.0																			Alger	McIntyre, 1931
27.8	21.1	44.0																			Alger	"
71.2	4.1	17.6					Give	n as	sq. f	t. pe	r acr	e, t	ansl	ated	into	per	cent				Alger	"
66.5	1.4		8.7		23.2																Alger	"
54.4	4.3		16.6		1.8																Alger	"
78.4	3.0		9.4		6.7																Alger	"
40.1	9.4	.3	1.7	17.7	.8																Part of tabulation by U. S. Forest Service	Cunningham, 1941
11.1	20.3		1.3	66.0	.24															W. Upper Mich.	Gogebic	Survey of 13,000 acres by Marathon Corporation
32.0	19.0		17.0	18.0	13.0															Wisconsin	Florence	Zon & Scholz, 1929
33.0	15.0		7.0	32.0	7.0	1.0					3.0								2.0	Wisconsin	Forest, Florence, Marinette	"
10.0	21.8			55.0																	Oconto	Duerr & Stoddard, 1938
23.5	17.0			58.0										1.0							Vilas	Potzger (Tab. 16-17)
20.4	17.0		.01	62.0																	Vilas	Potzger (Tab. 9-10)
10.1	16.0		6.0	72.4																	Price	Potzger (Tab. 6-7)
60.5			25.0		11.4						3.4									Minnesota	Minatonka	Daubenmire, 1936
46.2			25.7		7.6				2.3		3.0							11.3	.7		Northfield	"

PART II. HISTORY OF THE LAKE FOREST FORMATION

INTRODUCTION

It requires but small acquaintance with the lake forest to recognize that its vegetational complex differs from that of the forest formations to the north and to the south of it. While it embodies type species of both flanking formations it possesses an atmosphere all its own. Its early history is linked with frontiers of continental ice caps, and its development was associated with a poleward march of forests when moderating climate transformed ice masses of millennia of accumulations into rushing streams and countless lakes and ponds. Small wonder then that the march of individual and associations of species fired the imagination, and taxed the analytical capacities of plant geographers to read into the present the trails of the past.

Weaver and Clements (1938) define its location as follows, "As its name implies, this is preeminently a lake formation, being centered on the Great Lakes and recurring to the eastward in New York and New England where the larger lakes and rivers produced similar conditions."

Before the post-glacial history of the lake forest is considered it is perhaps essential to discuss some important characteristics and problems in this formation.

One reason why this formation plays such an important part in the literature dealing with forest formations, and why migration of its components occupies the attention of ecologists more intensely than other formations is no doubt the contrasting, disjunct, "non-sociable" distribution of broadleaved and coniferous species. The broadleaved forest to the south of it presents long lists of oaks and hickories, which are closely related to one another, and so similar in external appearance that their association is taken more for granted, and less thought is given to the origin of the association, or whether the associated species migrated from a common center at equal pace. Perhaps it might be said, too, that habitats in the south are more stabilized than the heterogeneous, at times poverty-stricken, soil complex of the lake forest region, and so the vegetation south of the lakes region is more stabilized.

The concept "plant association," too, is a much debated topic. The association is, after all, a dynamic unit which varies greatly, especially in the lake forest. No doubt this was a big factor in the formulation of Gleason's (1939) individualistic concept of the association. For the same reason it is perhaps so difficult to determine the climax for the lake forest. However, the pollen profiles mark clearly the successional changes which have replaced the transitional or tension zone southward of central Michigan, culminating in an association of broadleaved genera. The lake forest is a young formation, even now undergoing changes more rapidly than the deciduous forest which may some day obliterate it entirely in its present location, repeating the cycle which has already run its course farther southward (Figs. 9, 11). Above all, it is difficult to establish uniform characteristic abundance of the species constituting the association for the whole geographical extent of the lake forest because it varies more than the lake forest as a whole. This is quite apparent when one reviews the literature dealing with the forests of today, or when comparing upper sections of pollen spectra from bogs located in different parts of the formation. It is, of course, regrettable that many ecologists have not yet fully realized the importance of quantitative data on forest complexes, especially since more than a quarter century ago field men challenged antiquated, meaningless, generalized descriptions. In 1924 Merrill and Hawley wrote, "Unfortunately it is now too late to determine by direct observation and measurement the climax forest. No longer do examples of the original forest exist." Importance of such studies is pointed out by the same authors, saying, "To appraise correctly the relation existing to-day between hemlock and other forest trees, knowledge is essential as to the original forest condition." Lutz (1928) stresses the needs of silviculturists as follows, "Experience has demonstrated that after all silviculture which recognizes the tendencies of nature is the best silviculture." Foresters are much more alert to the real need of quantitative records than many ecologists, as the literature quoted here amply shows.

Mere descriptions are unsatisfactory for comparative purposes even today. Want of quantitative field work reduces the significance of publications for future use, and makes comparison with various sectors of a given formation impossible. Just to say, hemlock or maple is the most abundant, or, hemlock exceeds maple in abundance, means practically nothing. Unless a worker has actually made quantitative and qualitative field studies by means of sample plots, he does not know his forest. Unfortunately we are letting the last stands of primeval forest vanish without retaining a quantitative and qualitative record of the sociology which made and controlled the forest complex. Conard (1939) voices the same sentiments when he says, "The need and the promise of sociological studies in the northern coniferous forest of North America may be emphasized. Complete sociological analyses of these communities would lead to a better understanding of their biotic relationships." Cain (1939) stresses the same need when he says, "Mere lists of species cannot give more than a very poor idea of the complexity of a piece of vegetation. Every description of a plant community should consider the density, and manner of distribution of the plants of each species." The majority of papers on stands of the lake forest do not even present a list of species, and the arboreal layer is described only in a general, non-diagnostic manner.

The factors which determine a vegetation are also too frequently considered as single variables. Climate is no doubt the major determiner, but soil,

available moisture, evaporation deficit, acidity, effect of plant on plant, mycorrhiza, and last but not least, the physiological differences in a given phenotype, which Turesson (1929) calls ecotypes, play separate and collective vital parts in the distribution of plants, as discussed by Cain (1944) on page 5, and as described by Potzger (1941) for the forests on Mackinac Island and for Round Island, (1944) Michigan. *Picea glauca, Thuja occidentalis,* and *Abies balsamea* there germinate and develop well in mineral soil with a pH of 8.5, while in bogs on the lower peninsula of Michigan these same species, apparently at least, grow luxuriantly on peat with pH 5 or less.

Climatic extremes seem to level the facets of microclimate, as indicated in the pollen spectra by the Picea-Abies and succeeding Pinus periods. A more tolerant climate will in the lake forest give soil moisture greater control, close the association in the Pinus complex to deciduous invaders (Tables 1-5), or vice versa (Tables 6-15), but in certain complex habitat sites form new associations which may involve key species of the three bounding forest formations, segregate the less adaptive species of a preceding climax in relic colonies, make temporary associates of more adaptive members with invading groups, as *Pinus strobus* with *Acer saccharum, Betula lutea,* and Fagus (Livingston, 1903), or even associate pioneer genera like Picea and Abies with broadleaved genera like Tilia and Acer, as reported by Grant (1934) for Itasca County, Minnesota. This can be appreciated fully only if the archives of lake and bog deposits are consulted for a microsketch of the march of forests and individual genera during the thousands of years since post-glacial times (Figs. 6-29). Disjunct distribution within narrow geographical confines characterizes advancing (Potzger, 1941; Griggs, 1934) as well as retreating vegetation (Daubenmire, 1931; Lindsey, 1932; Friesner and Potzger, 1932, 1934). To paraphrase Shakespeare, vegetations do not advance as battalions but as single individuals. It is the miroclimate of physiography within a comparatively uniform macroclimate which makes determination of climax at times so difficult. When Lutz (1928) says of the forests of southern New England, "With changes of soil come minor changes of forest composition," he really describes conditions for the whole extent of the lake forest, as the present study shows for Wisconsin and Michigan (Tables 10, 12 & 14) as Gates (1926); Clayberg (1920); Harvey (1920); Quick (1923); and Livingston (1905) show for lower Michigan, Cunningham and White (1941); McIntyre (1931) for the upper peninsula of Michigan, and Alway and McMiller (1933) report for Minnesota.

In the rugged sections of Indiana Quercus-Carya and mixed mesophytic forests are selected by exposure of slope; their separation is along a line (Potzger, 1935; Potzger and Friesner, 1940). In northern Wisconsin, pines and deciduous forests express themselves similarly (Table 24). Gates (1926) says for Cheboygan County, Michigan that "on the better soils pine forests grade sharply into beech-maple."

Climax in the Lake Forest

From the previous discussion it can readily be seen that climax is not always readily determined. Weaver and Clements (1938) set up the hypothesis that "each climax is the direct expression of the climate; the climate is the cause and the climax is the effect. The climax must be the final test of the climate." They also preclude that all the climax dominants must belong to the same life form, since this indicates a similar response to climate and a long association with each other. They further rule out evergreens as proper dominants of the deciduous forest. It is easy to agree with the fundamental principle that the climax is climatically controlled, but the writer does not agree that all climax dominants must belong to the same sub-phylum. If Tsuga was the mesophytic representative of the Gymnosperms, I see no reason why it should not become a codominant in a mesophytic forest complex constituted primarily of Angiosperms. At least, there is no doubt that in the northern hardwoods this is the *modus operandi,* as shown by field surveys, and as emphasized in pollen spectra. Auer (quoted by Sears, 1942) comments on this same characteristic of Tsuga in Canada. In 28 profiles recording both Tsuga and Quercus, Tsuga follows Quercus.

Another criterion which these authors assume as basic is that "one or more of the dominants range well throughout the formation." This latter requirement is well met by all species of pines in this formation as well as by most of the dominants in the deciduous forest complex (*Acer saccharum, Betula lutea, Tilia americana,* and, except for Minnesota, this is also true for *Tsuga canadensis*). The real problem in determination of climax in the lake forest, thus, revolves around the two more or less sharply segregated association complexes, one consisting chiefly or entirely of pines, the other of broadleaved species associated with Tsuga.

Weaver and Clements (1938) state their views as follows: "The lake forest consists of a single association, in which *Pinus strobus, P. resinosa* and *Tsuga canadensis* are the climax dominants."

Nowhere within the lake forest is the status of climax perhaps more debated than in Minnesota. Stallard (1929) and Bergman (1923) champion a triple climax theory for Minnesota, viz. Pinus, deciduous forest, and prairie; they are of the opinion that the Pinus association represents the Pinus-Tsuga association which Weaver and Clements define as climax for the lake forest. Bergman (1923) states, however, that "in the southern part of the Pinus climax region the Acer-Tilia climax is becoming established in many places following the removal of pines by lumbering and burning," and "the deciduous forest always tends to advance and replace the prairie in many favorable situations." Grant (1934) and Buell and Gordon (1945) read into the vegetation of the Itasca County region a Picea-hardwoods climax. Daubenmire (1936), Kittredge (1934) definitely call the maple-basswood complex climax in Minnesota.

For the lake forest as a whole the opinions group about two lines of interpretation, one favoring the pine-hemlock complex as climax, the other favoring hemlock-northern hardwoods as climax, and pines participating in such crown cover as relics. This latter group consists chiefly of men who made more or less detailed quantitative field surveys. In the east Lutz (1928), Merrill and Hawley (1924) consider hardwoods-hemlock climax in southern New England. These same authors further point out that pine must be introduced and aided by suppression of aggressive broadleaved species in order to yield a stand of commercial value. Hemlock on the other hand, can cope with hardwood competition. Young (1934) is of the opinion that in New York Acer, Fagus, *Betula lutea*, Tsuga, and *Picea rubra* constitute climax cover. Lutz (1930) interprets the hemlock-deciduous forest the climax for Hearts Content in Pennsylvania. Whitford (1901), working in the upper peninsula of Michigan, not only defines the deciduous-hemlock association climax but definitely designates white pine in such associations as relics. More recently Cunningham and White (1941) designate hemlock in the upper peninsula of Michigan as a "tree of the climax forest, associated with maple, birch and elm." For the southern peninsula of Michigan the following field ecologists rate deciduous forest climax: Quick (1923); Kenoyer (1930, 1934); Gleason (1924). Harvey (1920) divides the forests of Lake County, Michigan into "climax forest (mixed hardwood association) and edaphic formation (needle-leaved evergreen forest)." He considers northeastern evergreen forest relic, which overlaps and intermingles with the deciduous climax forest.

For the whole region, Nichols (1935) says, "The climax favored by climate and the one which is generally developed on the better soils throughout the eastern hemlock region is a mesophytic forest comprising a mixture of evergreen conifers and deciduous broadleaf trees."

The author agrees with Grant (1934) that abundance of a given species or groups of species is not a safe criterion for determining climax (if we agree that a climax is climatically controlled). This is forcefully emphasized in pollen spectra in the "sudden" decline of Picea after Pinus once invaded, and in the ultimate extinction of Picea when Quercus made its appearance (Figs. 6-11). Physiographic control which perpetuates a former climatic climax is difficult to define, especially when it is not likely to change sufficiently in generations of men to permit control of the whole area by the "real" climax forest. Gates (1942) points out such control by bog habitats. Cunningham and White (1941) show this microclimatic effect on distribution of forest types in the upper peninsula of Michigan excellently in the fine colored map appended to their publication, for in an identical macroclimate Picea-Abies, Pinus, and northern deciduous forest adjoin within small geographical differences. However, results of studies in the northern hardwoods and records from pollen profiles convince me that Abies, Picea, and Pinus in the lake forest occupy a relic or post-climax status, and northern hardwoods (which includes Tsuga) have moved into climax position. (Figs. 14, 22-24.) The pollen spectra show clearly that Pinus declined from its former prominence but also that Tsuga, associated with broadleaved genera, superseded Pinus as the most recent invaders. One must consider as most significant that from Minnesota to southern New England, and northward of central Michigan the pine dominance controlled for a long period of time after replacement of the Picea period, indicating a climate which was unfavorable to the invasion by broadleaved genera (Figs. 12-29).

Descriptions and data from the broadleaved-hemlock stands representative of various sections of the lake forest impress one with the fidelity which nearly all of the most important species show throughout the whole range of the formation; differing, however, in abundance from place to place. The fluctuation in abundance is evident from state to state, and also within the geographical limits of any one state (Table 25). Lutz (1928) says that in the climax hemlock-hardwoods of northwestern Connecticut hemlock and beech constitute 55 percent, maple 12, yellow birch 1, red oak 6, chestnut 6, white ash and basswood 7. Westward, in New York, the composition changes, *Betula lutea* shows greater abundance. According to McCarthy and Belyea (1920) totalling 19.6 percent in a stand of 442 acres, while in a 700-acre tract in Herkhimer County it totalled 13.04 percent. Tsuga is less abundant, but red spruce plays a prominent role (27 percent). According to Lutz (1930) similar forest cover is climax in Pennsylvania, but Tsuga increases. Quantitative data from reports by foresters show that in Michigan Quercus and Fagus decrease in abundance from that to the east, while Tilia, *Acer saccharum*, and Ulmus become more prominent. For a fine description of the status along the tension zone in central lower Michigan see Livingston (1903) and for southwestern Wisconsin Marks (1942). In Kent County, Michigan Tsuga and *Betula lutea* have declined, or disappeared, on the favorable soils; *Pinus resinosa*, likewise, has disappeared, the competition on the drier sites is between *Pinus strobus* and the Quercus-Carya complex. The unique study by Kenoyer (1930, 1934) in the southern tier of counties in Michigan dovetails well into Livingston's (1903) work to show gradual replacement of Pinus by Quercus on the drier sites, replacement of Fagus-Acer-Tsuga by Fagus-Acer, and accentuated competition between the Fagus-Acer and Quercus-Carya types of broadleaved forests.

To the north (Vilas and Price Counties, Wisconsin and Gogebic County, Michigan) Quercus assumes the secondary role of the small tree stratum in the pine stands (Tables 1-4). Disappearance of Fagus and small representation of Ulmus is compensated by greater density of *Acer saccharum*, Tsuga, and perhaps *Betula lutea*. According to the quantitative

data of Daubenmire (1936) *Betula lutea* must be rare in Minnesota, while Tilia shows a pronounced increase in abundance. From reports by men like Shirley (1941) and Cunningham and White (1941) it is safe to conclude that the sharply separated Pinus and northern hardwoods associations found their most typical expression in the three centrally located Lakes States. Pinus occupied primarily the poorer sandy soils, and Tsuga-northern hardwoods the better clay and loam soils. For central-northern Wisconsin and western upper Michigan the quantitative data shown in Part I of the present study are perhaps a fair representation of the average conditions under which these associations operated.

Perusal of the literature, and a reference by Daubenmire (1936) to the variability in the abundance of the various leading species in the canopy of the climax forest when considering logitudinal geographical location suggested the thought that a graph (Fig. 31) based on averaged percentages of quantitative data ought to show the importance of the several associates, and possible variation in this respect, from New England to Minnesota. While New England, New York, and Pennsylvania are outside of the border proper set by Weaver and Clements (1938) for the lake forest, they were included in the graph because the associates in the climax forest there are strikingly similar to those about the Great Lakes. Authors from whose articles the percentage figures were obtained are listed in Table 25. For Pennsylvania the author included the percentages for the various species recorded in the field notes of the geological survey by Dale, as computed by Lutz (1930), representing 174,000 acres in northwestern Pennsylvania, because they agreed so closely with Lutz's (1930) careful ecological survey of Hearts Content.

To Mr. J. S. Landon, Marathon Corporation, Ironwood, Michigan, the writer is indebted for figures on the percentage representation of the various species in a 13,000 acre tract of northern hardwoods owned by his company in Gogebic County, Michigan.

While the percentage figures in the report by Cunningham and White (1941), based on the forest survey by the Lakes States Forest Experiment Station, involving the greater part of Michigan (13,000 sample plots of 2/10 acre each), as shown in Fig. 1, do not agree with the derived figures per se, which form the basis of this graph, there is agreement between the fluctuations in abundance of a given species in space, and differences in abundance between the various species. The graph for Quercus leaves much to be desired for accurate representation of the status quo, because in the eastern extension Quercus has on less favorable sites very likely taken over in a Quercus or Quercus-Carya forest cover the role of Pinus in the Lake States. Jennings (1909) describes such displacement of Pinus on Presque Isle, Pennsylvania, where *Quercus velutina* succeeds Pinus.

Skips between focal points in the graph are great, so that the peaks and troughs no doubt do not show the whole variation. In spite of such imperfections, and in spite of the limited amount of quantitative data on which the graphic presentation had to be based, the graph does show satisfactorily the uniformity of the northern hardwoods association, as well as variation in space in the abundance of the various dominants. Naturally, such a graph can only approximate the true status, however, it shows at a glance what Frothingham (1915), Daubenmire (1936), and others tried to express verbally.

Post-Glacial History of the Lake Forest

based on a philosophical and relic colony viewpoint

The most pretentious philosophical treatise on the origin of the formations on the North American continent is the one by Harshberger (1911). For the vegetation of New Jersey he envisioned Pinus as pioneer invader of ice-free soil which was replaced by broadleaved genera migrating northward along the river valleys from the southern Appalachians, and Picea and Tsuga as final invaders, migrating along the higher altitudes of the eastern mountains. For the eastern forest as a whole he states briefly: "A large number of species came from the great forest in which broadleaved and coniferous trees were intermingled, the latter were found especially perhaps during glacial times on the mountain tops which had remained undisturbed in their original home. The spread from the common center has been in a series of more or less concentric waves. The trees invaded the northern part of the continent approximately in the order indicated by their present relative distribution. Those farthest north entered first. In the Ohio valley the northern fringe of this deciduous forest encompassed the bog societies which here existed along the most southern lobe of the great ice sheet. Oaks, hickories, maples, ashes, elms followed the stream valleys or the uplands and surrounded the bog associations in their northward progression."

In a detailed map Transeau (1903) presents his conception of the vegetation adjacent to the ice lobes. He pictures a tundra bordering the ice rim, flanked by a broadleaved forest in which a few scattered conifers are associated. He expresses doubt that pine, spruce, and hemlock had ever been dominant in Ohio, Indiana, and southern Michigan. He says, "It seems probable that the conifers have reached their present distribution in the lower peninsula of Michigan by way of the lake shores. Probably the great bulk came by way of the southern end of Lake Michigan and from Ontario."

Quick (1923), quoting Transeau (1903) makes the terminating statement, "The conifers were not present in the Ohio valley, so that the deciduous trees and shrubs directly replaced the tundra and bog associations in the south and central part of Michigan."

Gleason (1923) describes the climate immediately south of the ice margin as warm "like in Tennessee and Arkansas to-day," and while the conifers of the present northeastern states migrated southward be-

fore the ice they "must have been reduced to a narrow strip between the ice margin and the deciduous forest, and the whole flora shifted northward with retreat of the ice." He concludes by saying, "Under this view we may assume that the Ohio valley in southern Indiana and Illinois was occupied by its present flora, possibly not so luxuriantly developed." He postulates a xerothermic period of comparatively recent times during which prairie vegetation expanded eastward, which limited the mesophytic species to a northward migration, while floodplain and xerophytic species migrated both north and westward. Likewise does he state that the morainal strip of boreal vegetation in the Middle West must always have been narrow and subject to frequent interruptions. To quote him further, "A northward movement of beech and maple and their associated species to their present location must have taken place after retreat of the ice, but the details of this migration must be discovered by other lines of evidence." Gleason is also of the opinion that every movement of vegetation must have left relic colonies behind it, whose perpetuation depends on the continuation of an environment not only favorable to the relic species but distinctly unfavorable to the invaders. In Minnesota he sees an entrance of the deciduous forest between the prairie and the coniferous forest, so that the prairie may never have extended much beyond its present range. He believes that during the xerothermic period the prairie advanced east and northward, following immediately behind the coniferous forest, during which time bogs were obliterated. The prairie first invaded Illinois, then Indiana, and finally extended its range northward to central Michigan and Wisconsin. According to this conception, succession between prairie and conifers was completed before the invasion by deciduous trees.

Dachnowski (1921), basing his arguments on characteristics of peat profiles, believes that Ohio experienced two comparatively dry and cool periods which alternated with relatively warm and humid periods.

Adams (1902) holds the view that the boreal forest formed a narrow belt and that "south of the Ohio during the ice age there was a diversified temperate flora and fauna; the temperate forms pushed close upon the rear of the arctic ones which fringed as a zone the edge of the ice." He pictures succession as stunted willows, birches and alders followed by pines, hemlock, spruce, and larch, which in turn were replaced by a third wave of oaks, hickories, ashes, maples, and walnut, which crept northward along fertile valleys.

BASED ON A PALEOBOTANICAL VIEWPOINT[2]

The treatises of a quarter century, or longer, ago, dealing with the history of the vegetation of eastern North America based much of their reasoning with reference to former plant migration and southward extention on distribution of relic plants, and on belting of forests of today. In the pollen profiles a more complete record is now available, at least with reference to the tree strata, which show not only succession of forests in a given locality but also the migration and development of formations. Since the lake forest is the central thought of this study it was naturally of prime importance to know how far southward this transitional type had found expression during post-glacial times. Figs. 6 to 14 represent a geographical difference of approximately 400 miles in latitudinal comparison, involving the southernmost borders of Early and Late Wisconsin glaciation. We find that the boreal forest period was uniformly the same from the southernmost border to the northern limits of the present lake forest, except that a greater number of foot-levels show control by the Picea-Abies period in Early and southern border of Late Wisconsin than in middle and upper Late Wisconsin territory (Compare Figs. 6-9 with Figs. 10, 11, 18-24). If Pinus-deciduous forest complex designates the lake forest type then we must conclude that this transition forest never developed well in Early Wisconsin territory in Indiana, was of comparatively short duration in lower reaches of Late Wisconsin territory in the central part of the eastern forest (Figs. 9 & 10) and increased in extent of control from lower Michigan (Fig. 11) northward in Michigan (Figs. 12-14) and Wisconsin (Figs. 18-24). It is rather interesting that from lower Michigan northward (Figs. 11-14, 18-24) and in New Jersey (Figs. 25-28), and Connecticut (Fig. 29) the boreal forest was succeeded primarily by Pinus, and the "dual" nature of the forest complex was a later development, or a result of succession.

If the presence of Betula (lutea?) and *Tsuga canadensis* is considered as indicators of the lake forest type, then it must be concluded that this transitional formation varied little in its geographical position from that of today, except that it extended farther eastward to New Jersey and southern New England. Tsuga is very sparingly represented in all pollen profiles from Indiana; and according to Sears (1942) also in Ohio, Illinois, and southern Michigan. Recent pollen studies by the writer (MS.) along the tension zone between Saginaw and Muskegon, Michigan show that Tsuga played only a minor role in forests south of a line crossing Farwell and Shelby, Michigan.

The greater number of foot-levels showing control by Picea and Abies in Early Wisconsin and southern fringe of Late Wisconsin territory indicates a wide belt of conifers south of the glacial border, which broadleaved species had not replaced before advance of the ice sheet known as Late Wisconsin (at least there was no return to boreal forest after deciduous forest invaded and replaced the Picea period). A wide belt of conifers along the southern border of the ice masses is also indicated (indirectly) by the

[2] Thanks is expressed to all authors whose profiles were previously published in other journals and are used in the present study. For complete citation see Literature Cited. Fig. 6, Otto (1938); Fig. 7, Howell (1938); Figs. 8, 10, Keller (1943); Figs. 9, 11, Potzger and Wilson (1941); Fig. 14, Wilson and Potzger (1943); Fig. 17, Wilson and Potzger (1943); Figs. 18, 19, Potzger (1943); Fig. 20, Potzger and Richards (1942); Figs. 23, 24, Potzger (1942); Figs. 25, 26, 27, 28, Potzger and Otto (1943); Fig. 29, Deevey (1943); Fig. 30, Potzger (1945).

recent discovery of pollen from Picea and Abies in the lower levels of the Patschke Bog in Texas (Potzger and Tharp, 1943), and discovery of macrofossils of boreal trees in Louisiana by Brown (1938). The Texas station is fully 800 miles south of the Ohio Valley region. The pollen profiles from Indiana (Figs. 6-10), lower Michigan (Fig. 11), and southeastern Minnesota (Fig. 17) give no evidence of a pronounced xerothermic period in which grasses completely replaced forest, neither is there to date any evidence that bogs in northwestern Indiana and lower Michigan were completely obliterated during an extreme xerothermic period, unless one would be justified to read such a phenomenon into the sudden decline of Picea without a comparable increase in grass pollens, definitely established as that contributed by prairie grasses. However, one would then be forced to include the eastern states bordering on the Atlantic. There is no evidence of replacement of coniferous forest by prairie in Anoka County (Fig. 17) and Hubbard County, Minnesota (Figs. 15 & 16), however, in Hubbard County Quercus had extended a controlling influence farther eastward than it has today, and was replaced again by Pinus. Succession in the Minnesota area is therefore in part like that in upper Wisconsin and Michigan and in part like that in Indiana.

Bogs and lakes located in areas of better loam soils in Michigan (Fig. 11), Wisconsin (Figs. 22-24), New Jersey (Figs. 25-28), and according to Deevey (1943) in Connecticut (Fig. 29) show in their pollen profiles that Tsuga was always associated with broadleaved genera, it definitely belonged to the association which succeeded the Pinus period. This points to the conclusion that Tsuga-deciduous forest are climax in the lake forest, and that Pinus represents post-climax, maintained by microclimate of habitat factors.

Recent work by the author (Fig. 30) on peat from bogs in the Pine Barrens of New Jersey suggests the thought that south of the Ohio valley was not the only center of northward distribution of the northeastern flora. The unglaciated Pine Barrens of New Jersey (Fig. 30) was very likely a more northerly refugium. Fig. 30 pictures a mixed forest whose components were *Picea glauca, P. mariana,* Pinus spp.?, Quercus spp.?, Carya, Ulmus, Tilia, Liquidambar, Salix, Ilex, Ericads, Tsuga, Castanea, Fagus, etc., crouching on the ice-free portion of New Jersey, invading northward (Figs. 25-28) in wave-like migrations, each successive wave of genera replacing the former, in which Carya and Castanea constituted the most recent invaders. Perchance, much of the Atlantic border areas of the north and west of New Jersey were vegetated from this center, so that while the lake forest type involved areas of more central as well as the northeastern states the centers of origin were not the same.

Discussion

Even though the opinion of the field analysts working in the lake forest is almost unanimous that northern hardwoods-Tsuga, or northern hardwoods in the western extension, are climax in the lake forest, it is perhaps not out of place to refer to this feature of the formation again. The pollen profiles (Figs. 6-29) show clearly how the process of replacement and ultimate elimination of a past climax operates. From central Indiana to the upper peninsula of Michigan climatic fluctuation was apparently slight, at least not sufficient to involve great changes in forest cover (Figs. 6-14). When Pinus crowded in, Picea was definitely being replaced, and once Quercus, or in Wisconsin, Michigan, and New Jersey the deciduous species associated with Tsuga appeared, Pinus began to decline (Figs. 9, 14, 17, 22-29). South of the lake forest of today replacement continued to small relic colonies of *Pinus strobus* (Fig. 1), or complete extinction. In a limited number of stations in Indiana such relic colonies persist under precarious conditions to the present day. Some of these communities have been described in detail by Lindsey (1932), Friesner and Potzger (1934), and Daubenmire (1931). It is, thus, very apparent that climatically favored species may at first be inferior in abundance, but they are climax nevertheless. Cooper (1913) has expressed this well when he says, "Wherever the sugar maple occurs it forms a part of the climax forest." The writer agrees with Grant (1934) that it is not the number which determines the climax status, but one must be certain, on the other hand, that he is dealing with climax and not post-climax. The pollen profiles from Hubbard County, Minnesota certainly raise some doubt as to the climax status of *Picea glauca* in Itaska County. Only if a climatic change has taken place can a post-climax species, even though it is in minority numerically, give the promise of expressing its dominance by increasing abundance. The two pollen profiles from Hubbard County (Figs. 15 & 16) clearly show the waning of Picea as a climax dominant in that part of Minnesota, and unless a climatic reversal (not evident in the pollen profile) is assumed it will be necessary to agree with Kittredge (1934) and Daubenmire (1936) that broadleaved forest (Acer, Tilia, Ulmus) is climax in Minnesota, which has replaced the former Pinus climax, which in its time had succeeded the Picea period. Picea held undisputed dominance in all areas from central Indiana to the Lakes States, and in the latter area yielded to a long, almost undisputed Pinus climax. Unfortunately the writer has no pollen record from the "Big Woods" area of Minnesota where the better soils are occupied by the basswood-maple association, but all pollen profiles from eastern and central states show that when Pinus enters the forest complex Picea loses control as climax (Figs. 6-29). Of course, local microclimatic factors may perpetuate control of crown cover by Picea as shown by Potzger (1941, 1944) for the peripheral areas of Mackinac and Round Islands, Michigan. Confronted by a similar condition in the forests of Itasca Park, Minnesota, Buell and Gordon (1945) attempt to establish as the criterion for determination

of climax the "competitive ability" of the species involved. It seems to the writer that such a criterion would never operate unless the concept "climax" were removed from climatic control, and edaphic factors were substituted. The small colonies of *Pinus strobus* and Tsuga in Indiana compete well with southern broadleaved forest in the areas they have occupied for a long time, yet it is doubtful if they would ever be called climax. As pointed out before, on Mackinac Island and Round Island, Michigan (Potzger 1941, 1944) spruce-fir is limited to a narrow peripheral belt, this is in direct contact with the beech-maple association and competes well with it. Macroclimate is no doubt identical in these two sharply separated forest types and so microclimatic factors make the selection. The polyclimax theory of Kell (1938), Bergman (1923), and Stallard (1929) would replace macroclimate as the sole determiner by other environmental factors but would of necessity also invalidate the post-climax and relic concept. The writer feels certain that if the lake forest region were more universally heavier clay and loam soils, as is characteristic of the soils of Indiana, the post-climax pine association would no longer maintain itself but would have yielded to northern hardwoods, as it has under present conditions on the better soils of Michigan, Wisconsin and Minnesota.

As pointed out in Part I of this paper, climatic climax does not necessarily mean inhibition of growth of less tolerant tree invaders, for it is quite evident that during the long Pinus period (Figs. 11-29) many generations of forests were produced, even though reproduction under closed crown cover was as impossible for the pines then as now. Open places, however, were then not occupied by saplings of tolerant species which excluded a start by pine when the opening was made by the fall of an old tree.

The significance of ecotypes, or biotypes, is given weighty consideration by Raup (1941) as an important factor in the migration of species. He believes that migration during Pleistocene times was not merely a displacement in space but also a selective influence on the biological character of the vegetation mass. According to such a concept it would be unlikely that vegetation moved southward as the identical mass of biotypes of a given phenotype. Only the more adaptive biotypes were able to meet the migration pressure, the less plastic types could not cope with the new conditions of habitat and competition in new associations, and so, no doubt, perished with annihilation of their habitat. The process of such annihilation is excellently pictured by Cooper (1942). Halliday and Brown (1943) share this opinion. The enlightening discoveries of cytotaxonomy during the very recent past stamps such a concept not as probable but rather as almost certain.

While pollen studies of Pleistocene deposits do not readily yield themselves to such sensitive differentiation of phenotypes, one does encounter at times pollens which show very striking variations from the "standard" design, as for instance an extremely large pollen of Abies with unusually peculiar attachment of wings which appeared in the sediments from Tippecanoe Lake (Fig. 9) and in several bogs from northern Wisconsin. In a private communication, L. R. Wilson also referred to this peculiar pollen type.

Raup (1941), Halliday and Brown (1943), and Sears (1942) also postulate several centers of dispersal for the present complex of the lake forest, instead of only the one southeastern forest center so commonly assumed by early plant geographers. Involved are, especially, the Driftless area (Sears, 1942) and exposed areas of the eastern continental shelf. Halliday and Brown (1943) are of the opinion that *Betula lutea* migrated westward from an eastern center. As pointed out earlier, the recent pollen studies in the Pine Barrens (Potzger, 1945) add concrete evidence to such an assumption.

Apparently it is erroneous to assume that Picea and Abies were scattered individuals in the mass of the deciduous forest crouching in the Ohio Valley. All pollen profiles from Early Wisconsin and lower Late Wisconsin areas in Indiana show a long time, almost complete dominance by *Picea glauca,* usually involving seven to ten foot-levels (Figs. 6-9). Apparently the spruce-fir forest was depressed very much farther south than Transeau (1903), Gleason (1923), Adams (1902), and Harshberger (1911) postulated, as the five percent pollen of Abies and *Picea glauca* reported by Potzger and Tharp (1943) from the Patschke Bog in Texas show, and as the macrofossils of Thuja and *Picea glauca* reported by Brown (1938) from Louisiana indicate. Not only is it difficult, if not impossible, to fit the pollen records (Figs. 25-29) into Harshberger's (1911) conception that the boreal species were found primarily on the mountain tops as a mixed association with broadleaved genera, it is, likewise, almost impossible to read into them a condition where broadleaved forest surrounded the bog societies at the southern limits of glaciation in Indiana. This is indicated when bogs had filled about 50 percent of the total depths. Facts deduced from the pollen profiles from Bacons Swamp (Fig. 6), the Hendricks County ancient lake studied by Potzger (1943) also do not coincide with Transeau's (1903) theory that "a few scattered conifers were associated with the mass of broadleaved forest adjacent to the ice lobes." Both of the previously named pollen studies show such a culminating Picea control for a long period of time that a mixed forest can hardly be read into the records. Certainly, we know now that spruce was the first invader and formed a dominant consociation from the southern limits of Early Wisconsin glaciation northward, and pine succeeded spruce in regions north of northern Indiana, expanding time of dominance on the northward migration, but also showing a fair representation as far south as Bacons Swamp. In the southern limits (Figs. 6-8) one must read into the record a pine-deciduous forest complex rather than a pine

consociation as in northern Indiana and Michigan. The pollen profiles, however, agree perfectly with Transeau's (1903) idea of the status of Tsuga in Indiana.

It appears that Quick (1923) had hardly sufficient grounds to make the unqualified, definite statement that "conifers were not present in the Ohio valley," and that "deciduous trees directly replaced the tundra and bog association in the southern and central part of Michigan." All pollen profiles from Hendricks County, Indiana to Third Sister Lake in southern Michigan reply in the negative to such a statement.

Gleason (1923) comes closer to a description in agreement with pollen profiles of forest conditions along the southern margin of the ice sheet when he pictures a narrow strip of forest where conifers of the present forests of the northeast dominated. However, the belt of boreal and semi-boreal trees could not have been so very narrow, otherwise one can hardly explain the long dominance by Picea. It would also be difficult to fit *Picea glauca* and Abies into the forests of Texas, even though one assumed southward migration of boreal species down the wide belt of microclimate in the Mississippi valley, cooled by the masses of glacial melt waters which the great river must have carried. Harshberger (1911), too, pushes the deciduous forest too close to the ice margin when he assumes that in the Ohio valley it "encompassed" the bog societies. The type of forest postulated for the border areas in Indiana, Potzger (1945) finds in pollen profiles south of the glacial boundary in New Jersey.

The lack of evidence in all pollen profiles from Indiana for so extreme a prairie invasion as pictured by Gleason (1923) and Transeau (1903) suggests the probability that prairie never completely replaced trees in its eastern extension in Indiana. Not a single bog studied to date shows dominance by grasses over trees, specifically oak. This is also true for Anoka County, Minnesota (Fig. 17) and Hubbard County, Minnesota (Figs. 15, 16). At both locations Picea was replaced by Pinus and this by a Pinus-Quercus association. However, in western Minnesota Quercus was later depressed by Pinus to an insignificant percentage. Conditions shown there agree with Gleason's (1923) thought that "in Minnesota the prairie may never have extended beyond its present range."

The migration of Fagus and Acer is not so clearly defined in the pollen profiles, however, Fagus shows greater abundance northward of southern Michigan. Acer, an insect-pollinated genus, is no doubt always under-represented in the pollen profiles. The apparent later invasion by Acer and Fagus in Indiana than in Michigan suggests the probability of a westward migration from eastern centers (Pine Barrens of New Jersey) or as Sears (1942) suggests from a western center in the Driftless area. However, it may also mean a more rapid segregation to the north of the belt of extreme Quercus competition.

Summary and Conclusions to Part II

1. Part II discusses briefly the controversies on what constitutes climax in the lake forest. It is shown that opinions are divided into two major groups. One considers pine-hemlock, the other hemlock-deciduous forest the climax. The latter group interprets Pinus on sandy soil post-climax, or edaphic climax. The writer shares the opinion of the latter group of workers.

2. Pollen profiles very definitely indicate that Pinus represents post-climax, and Tsuga associated with broadleaved genera represents climax. Twenty-five pollen profiles are presented.

3. Comparison is made between post-glacial history of the formation (lake forest) based on philosophical and relic colony theories and paleobotanical evidence.

4. Pollen profiles show that Picea constituted a belt between the ice front and the deciduous forest to the south in the interior location represented by Indiana. While no definite evidence is available at present by which to know the width of the belt of coniferous forest, the long period of almost complete dominance by *Picea glauca,* as well as the recent discovery of *Picea glauca* and Abies pollens in the Patschke Bog in Texas, indicate the likelihood that it was a wide rather than a narrow belt, as has been postulated by some students of plant geography.

5. If the Tsuga-broadleaved association is the criterion for defining the lake forest type, this formation has not shifted much from the position it holds today. If pine-deciduous forest (especially oak) are to be considered indicators then the southward range of this formation coincides with limits of Late Wisconsin glaciation.

6. A figure is included to show variation in abundance of the various species of trees in the climax forest complex from New England to Minnesota. The graph is based on averages of quantitative field data.

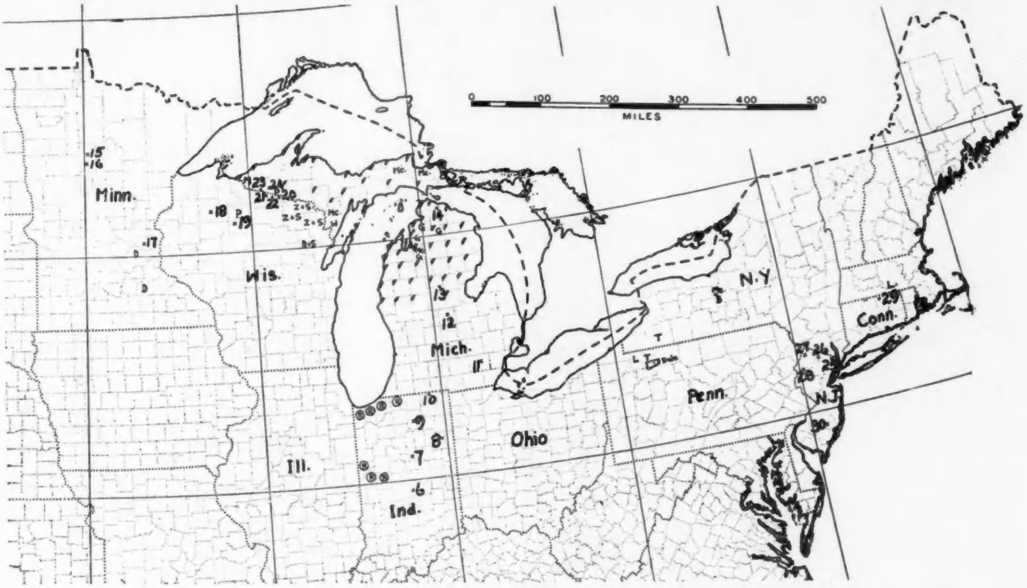


FIG. 1. Map of U. S. showing lake forest and loca ion cf courties where forest surveys and pollen studies were made.

Figures indicate location of pollen profiles, R in circle indicates relic colonies of *Pinus strobus*. Two short parallel lines indicate counties included in the U. S. forest survey. Data were used in construction of Fig. 31.

Initials refer to workers whose data were embodied in Fig. 31. They are: D (Daubenmire); D and S (Duerr and Stoddard); G (Gleason); L (Lutz); M (Marathon Corporation); Mc and B (McCarthy and Belyea); Mc (McIntyre); P (Potzger); T (Taylor); W (Westveld); Z and S (Zon and Scholz).

FIG. 2. *Pinus resinosa* stand at Point Woods.

FIG. 3. Crowns of pines at Point Woods.

Fig. 4. *Pinus strobus stand*, Dairymen's Country Club.

Fig. 5. Caro northern hardwoods stand.

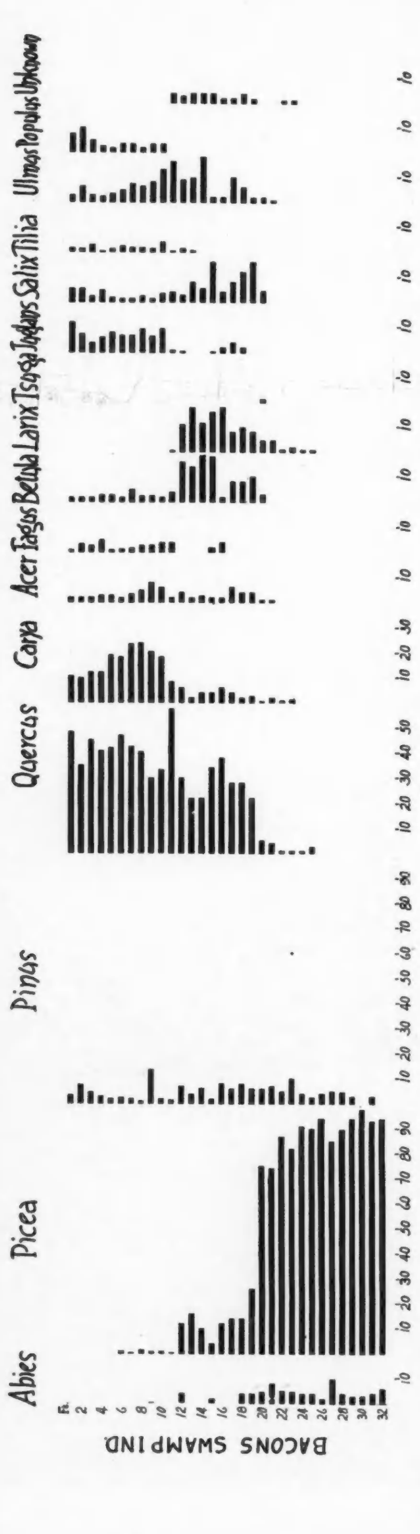


Fig. 6. Pollen profile from Bacon's Swamp, Indiana, showing percentage representation of various genera to indicate change in climate and climax.

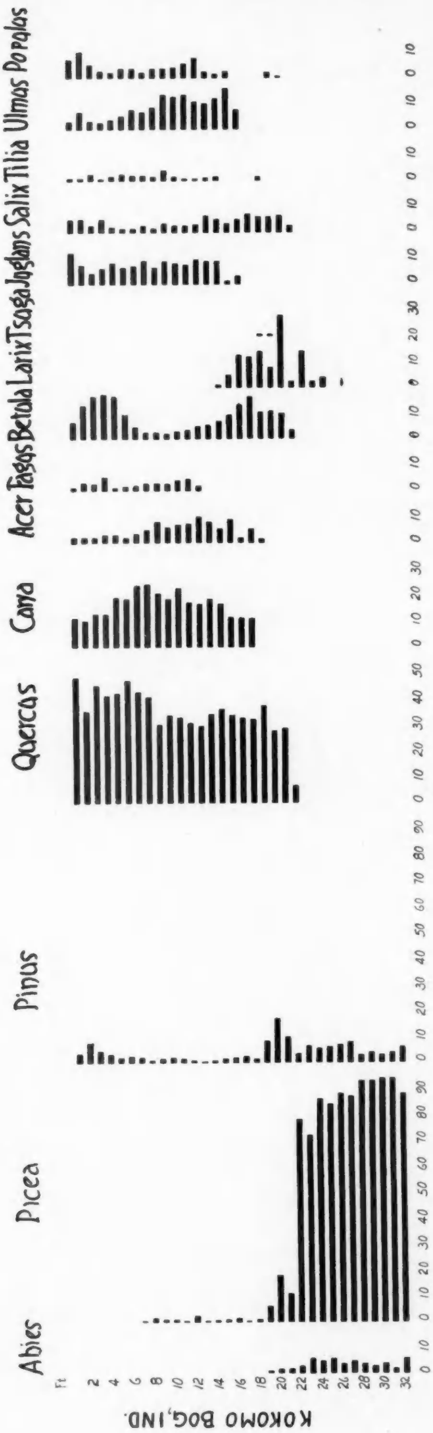


FIG. 7. Pollen profile from Kokomo Bog, Indiana, showing percentage representation of various genera to indicate change in climate and climax.

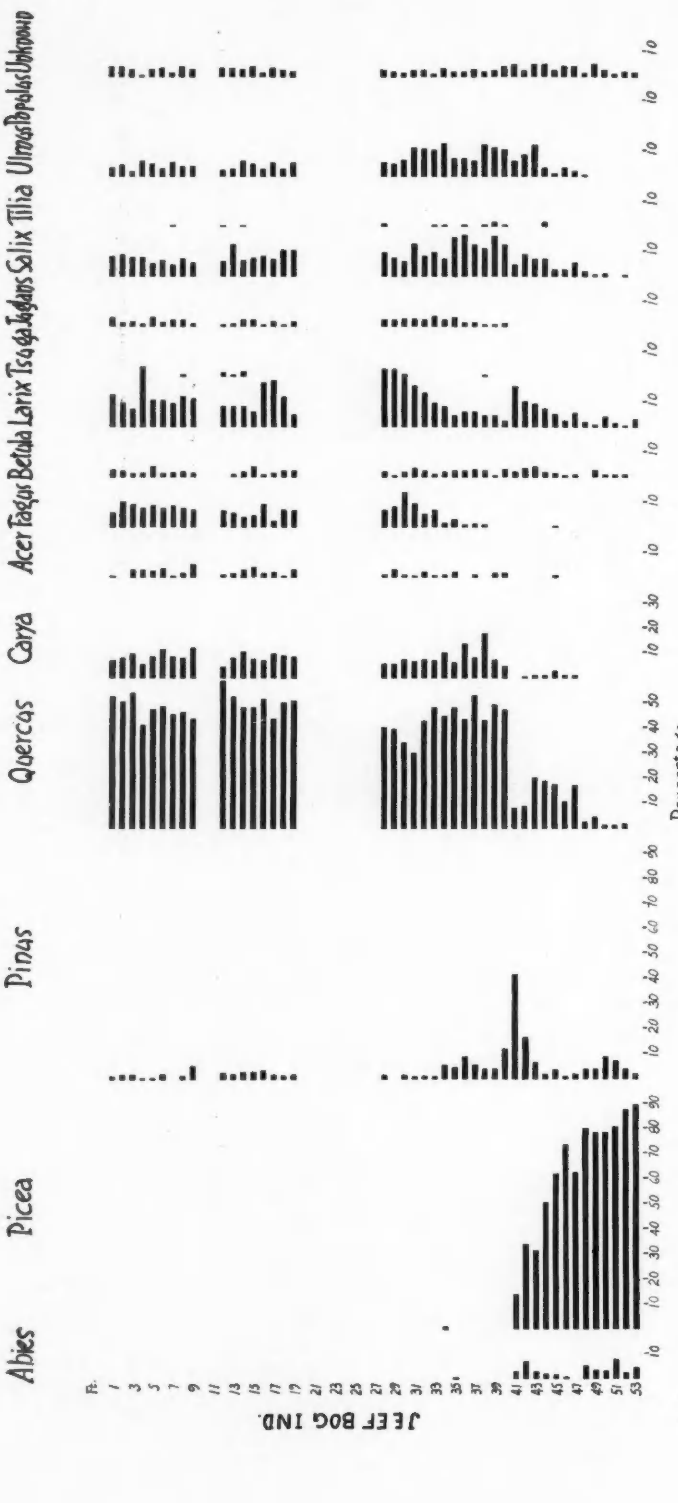


Fig. 8. Pollen profile from Jeff Bog, Indiana, showing percentage representation of various genera to indicate change in climate and climax.

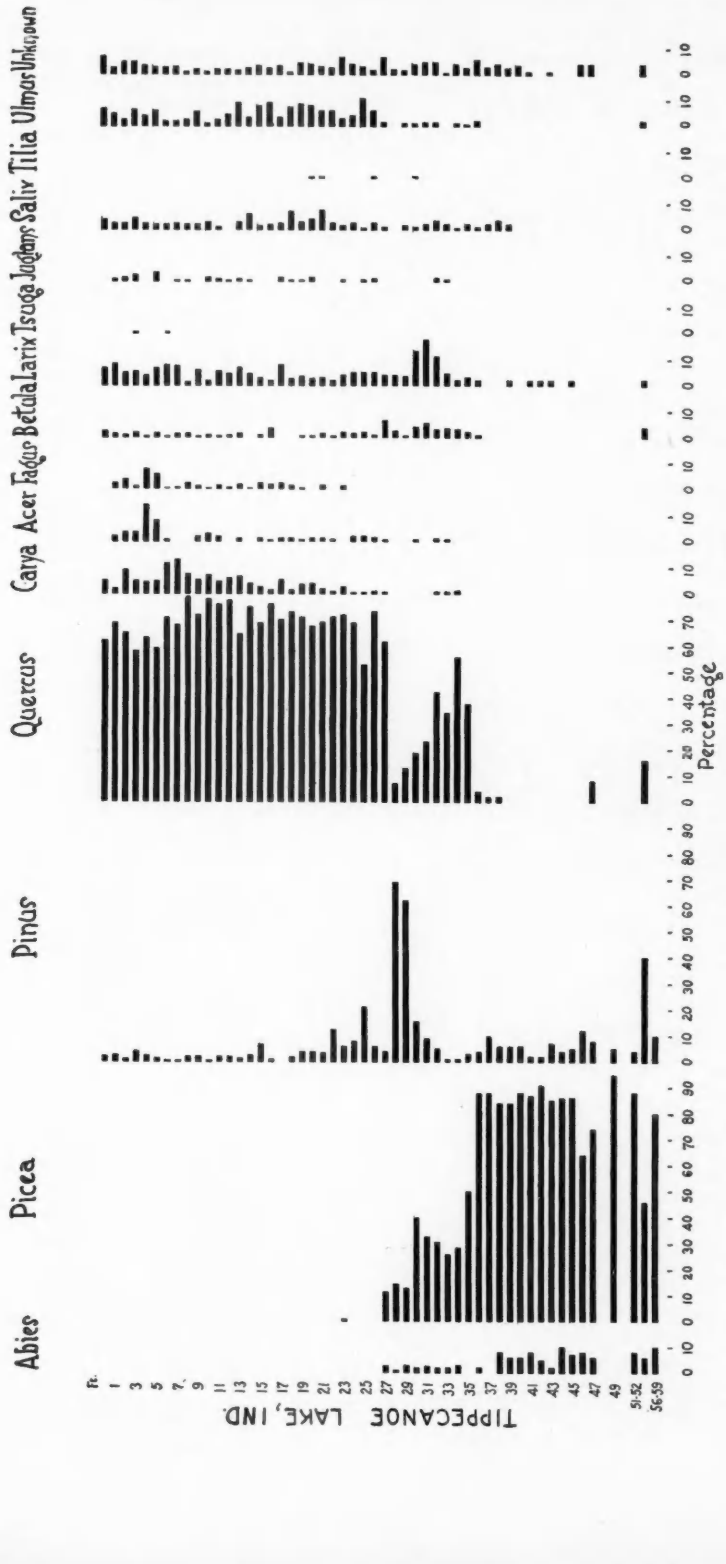
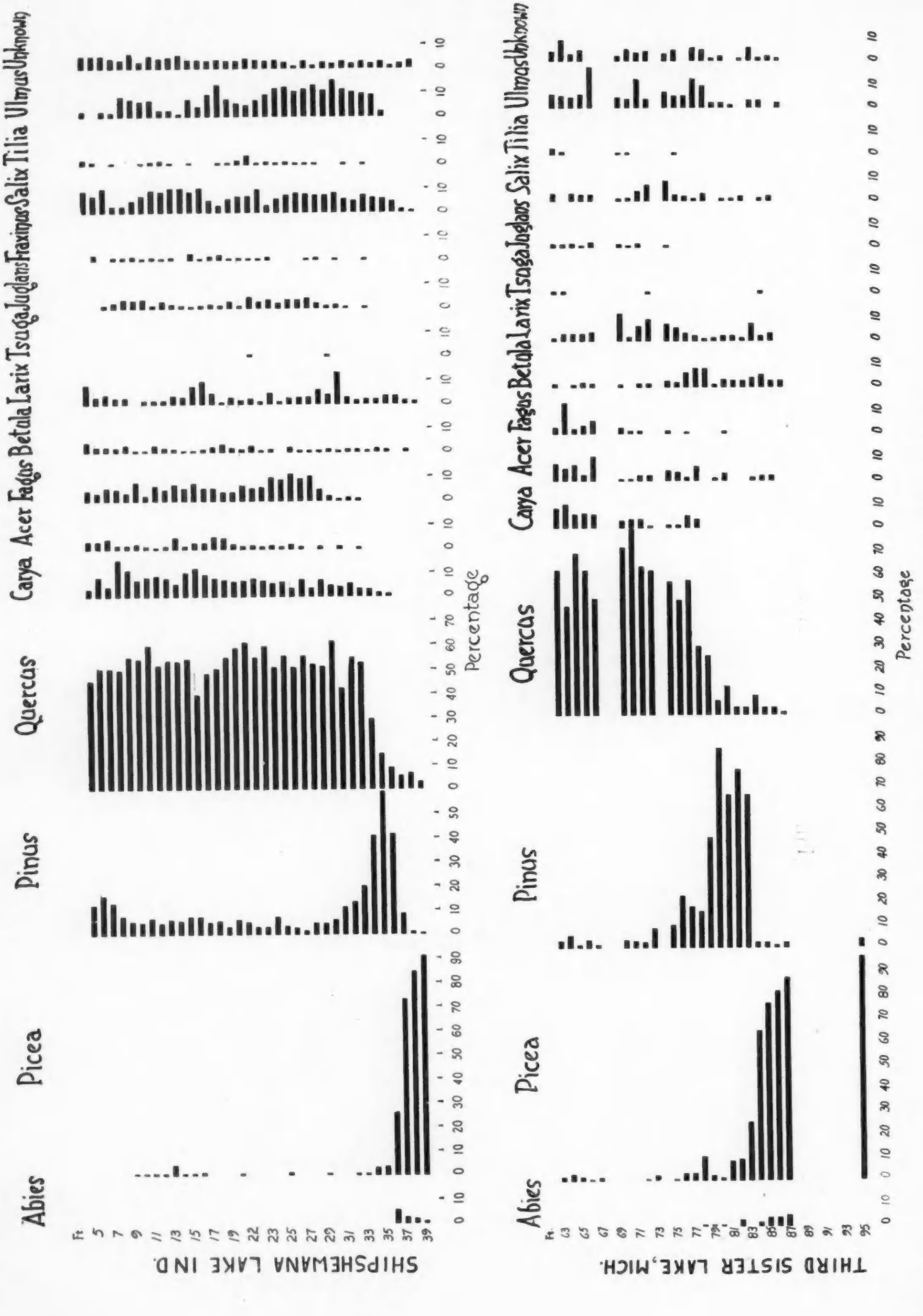


FIG. 9. Pollen profile from Tippecanoe Lake, Indiana, showing percentage representation of various genera to indicate change in climate and climax.



FIGS. 10 and 11. Pollen profiles typical of southern Michigan.

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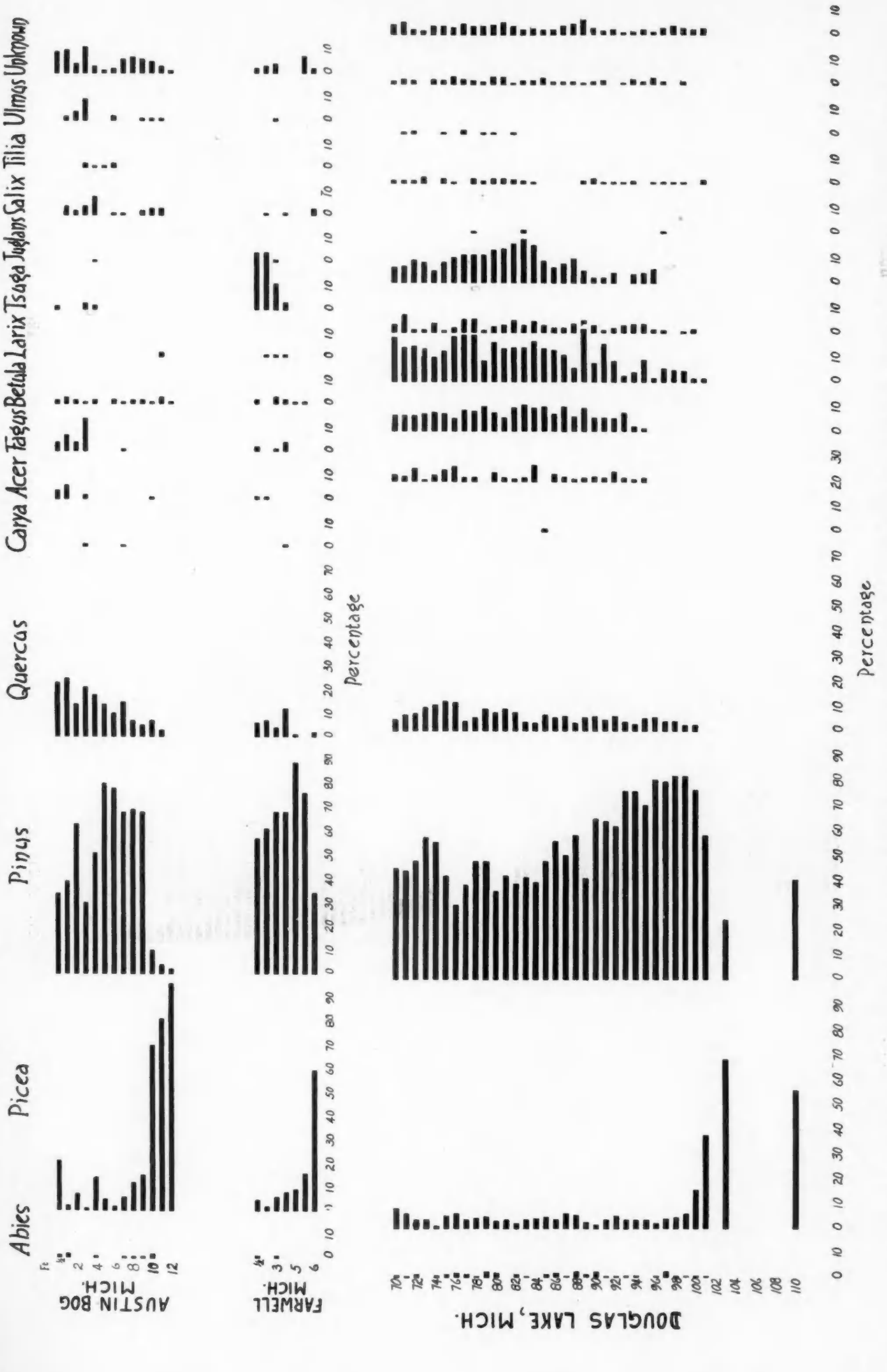
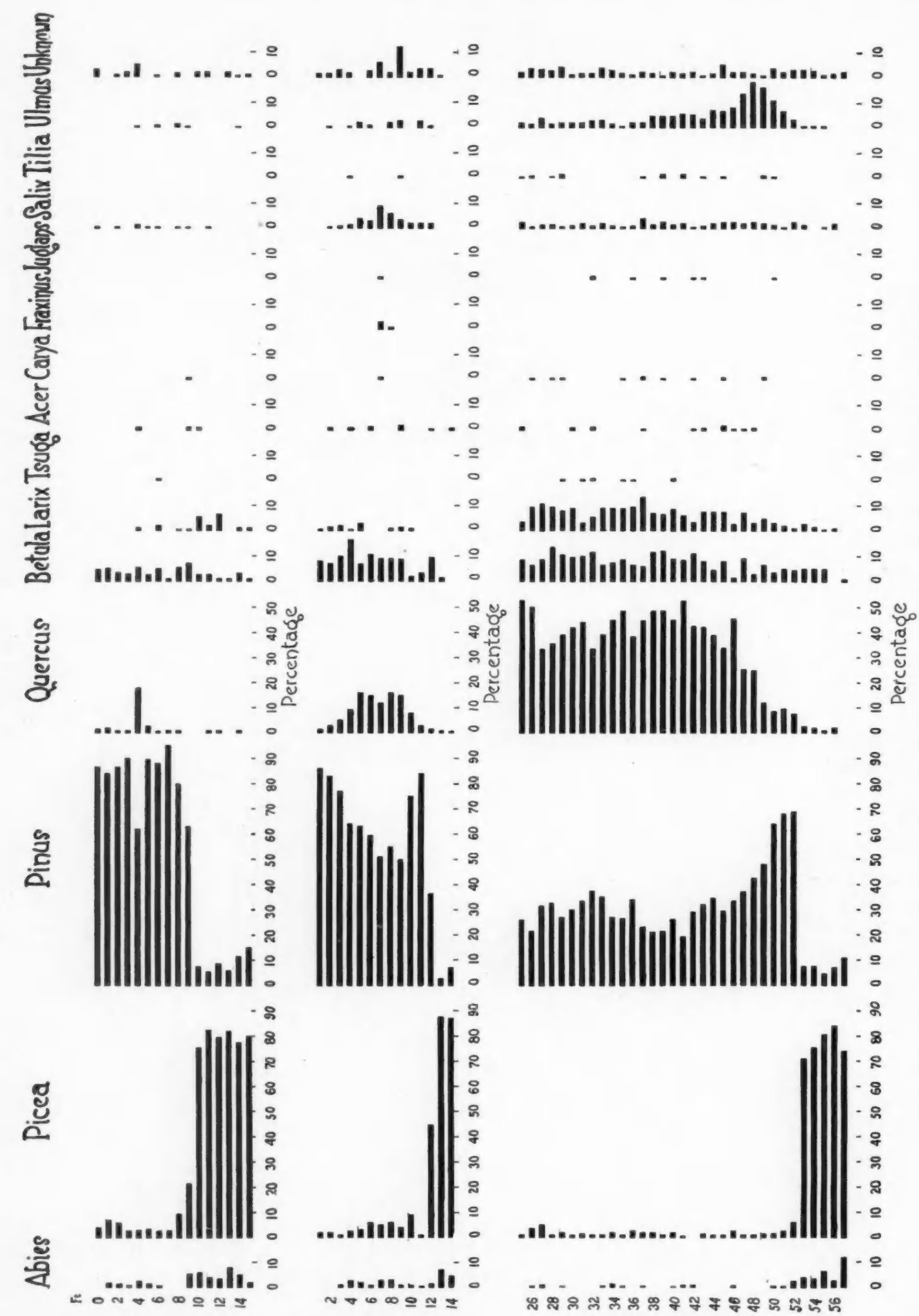
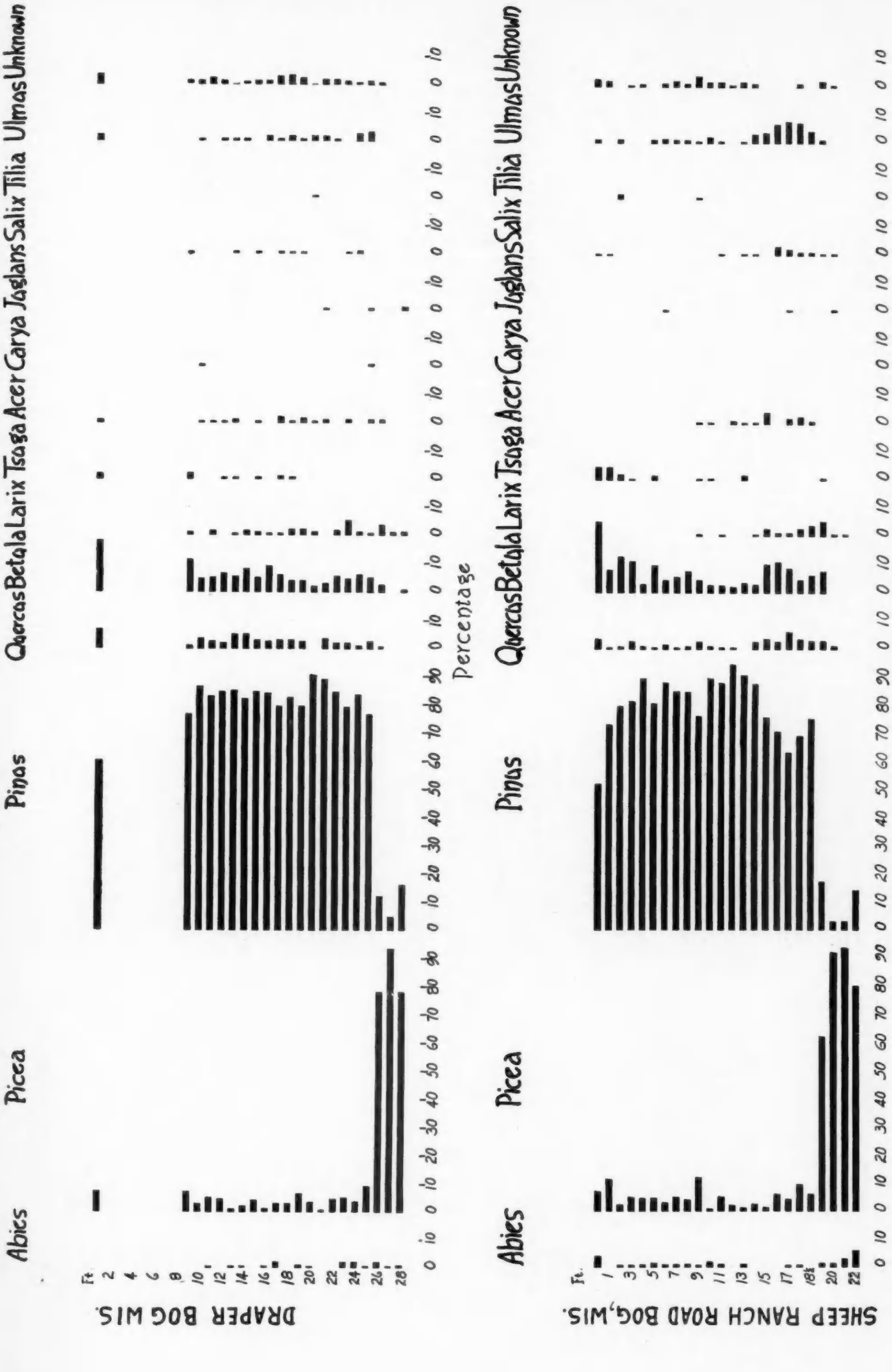


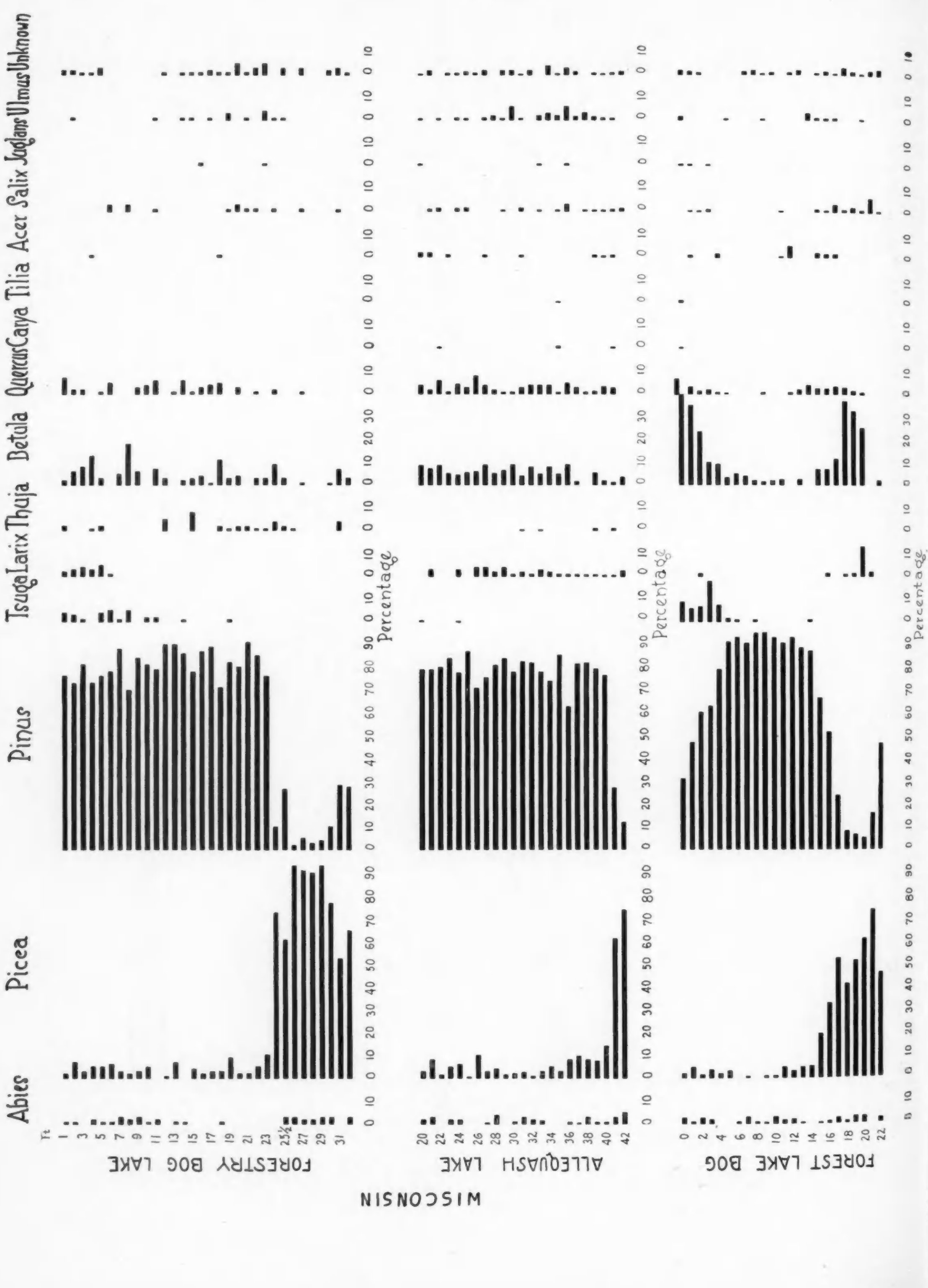
FIGS. 12, 13, and 14. Pollen profiles typical of central and northern Michigan. These figures and Figs. 10 and 11 show forest succession from southern to northern Michigan. Special features are increase of time during which pine dominated and decrease of time for oak dominance.

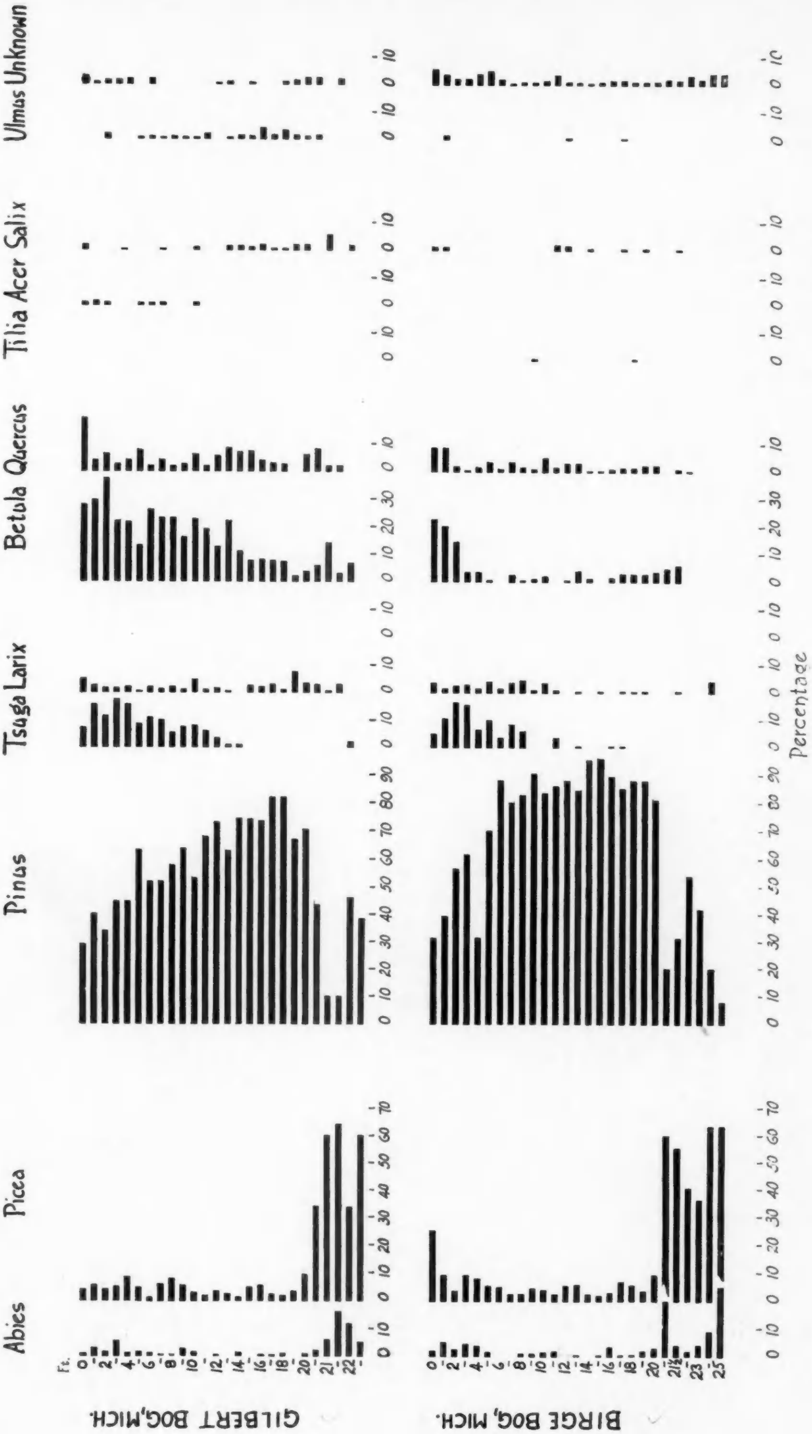


Figs. 15, 16, and 17. Pollen profiles for Hubbard Lake Bog, Henzel Bog, and Crooked Lake, Minn.

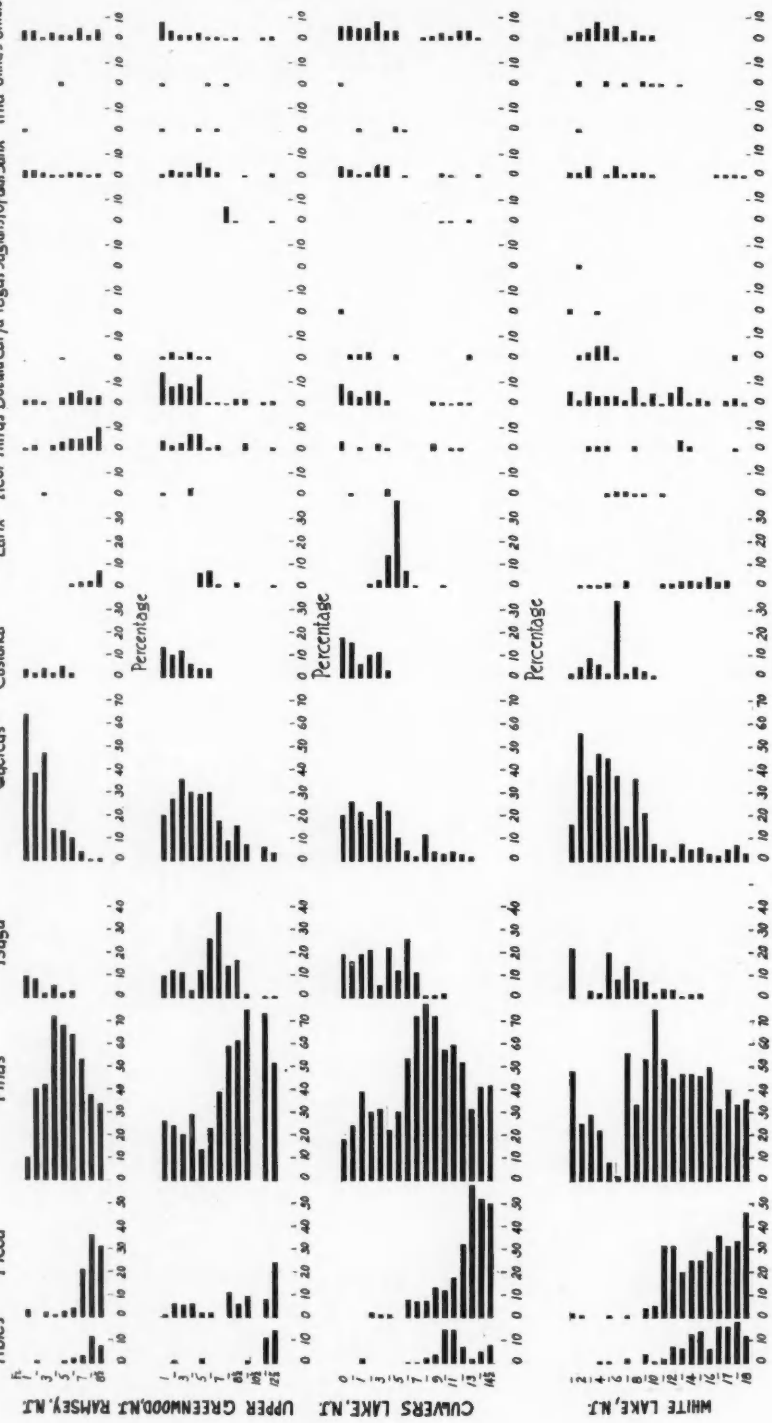


FIGS. 18 and 19. Pollen profiles for Draper Bog and Sheep Ranch Road Bog, Wis. These figures and Figs. 15, 16, and 17 show succession of forests in an area bounded by western Minnesota and central Upper Wisconsin.

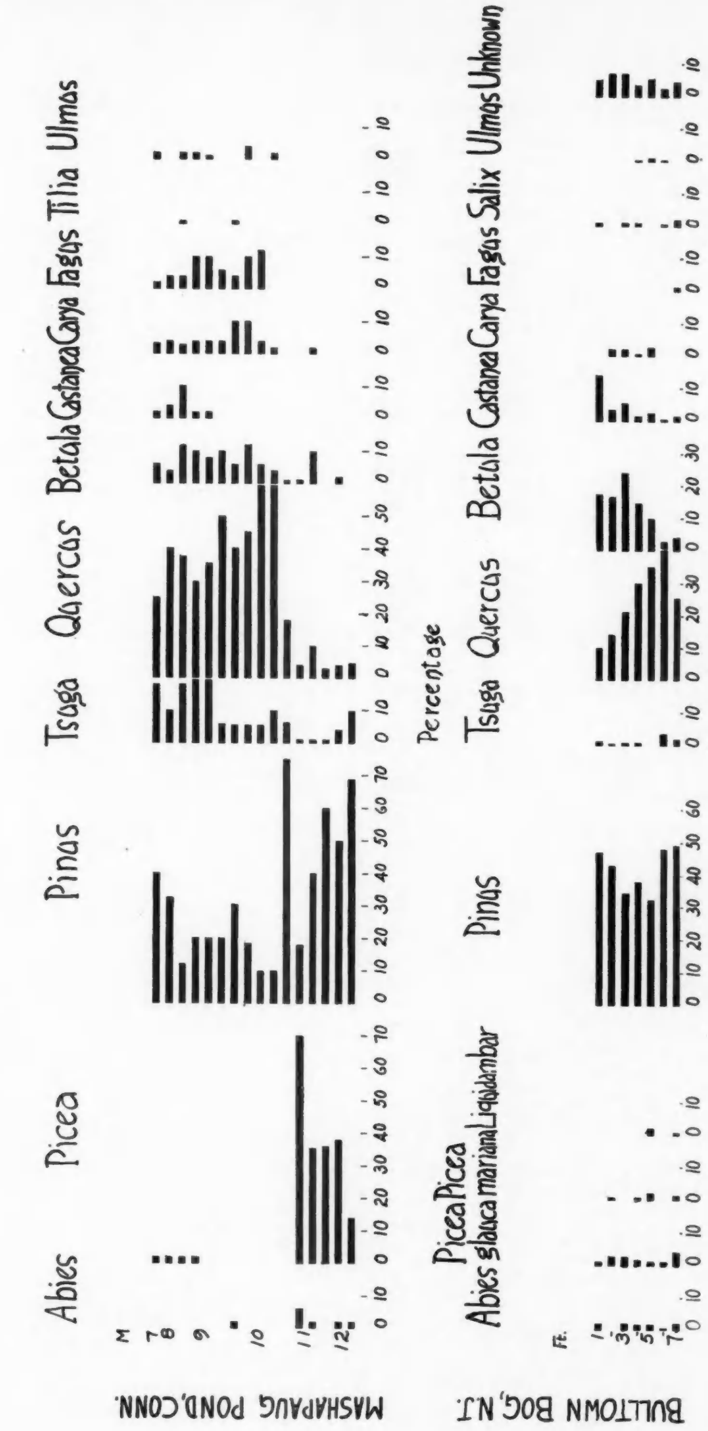

Abies
Picea
Pinus
Tsuga
Larix
Thuja
Betula
Quercus
Carya
Tilia
Acer
Salix
Juglans
Ulmus
Unknown
Percentage
FORESTRY BOG LAKE
ALLEQUASH LAKE
FOREST LAKE BOG
WISCONSIN



FIGS. 23 and 24. Pollen profiles for Gilbert Bog and Birge Bog, Mich. These figures and Figs. 20, 21, and 22 show succession and origin of the hemlock-deciduous forest association in the lake forest and with Figs. 15-22 show persistence of the earlier universal pine dominance in areas characterized by sandy soil.



Figs. 25-28. Pollen profiles from glaciated New Jersey.



FIGS. 29-30. Pollen profiles from Mashapaug Pond, Conn., and from Bulltown Bog, N. J., the latter in the unglaciated pine barrens.

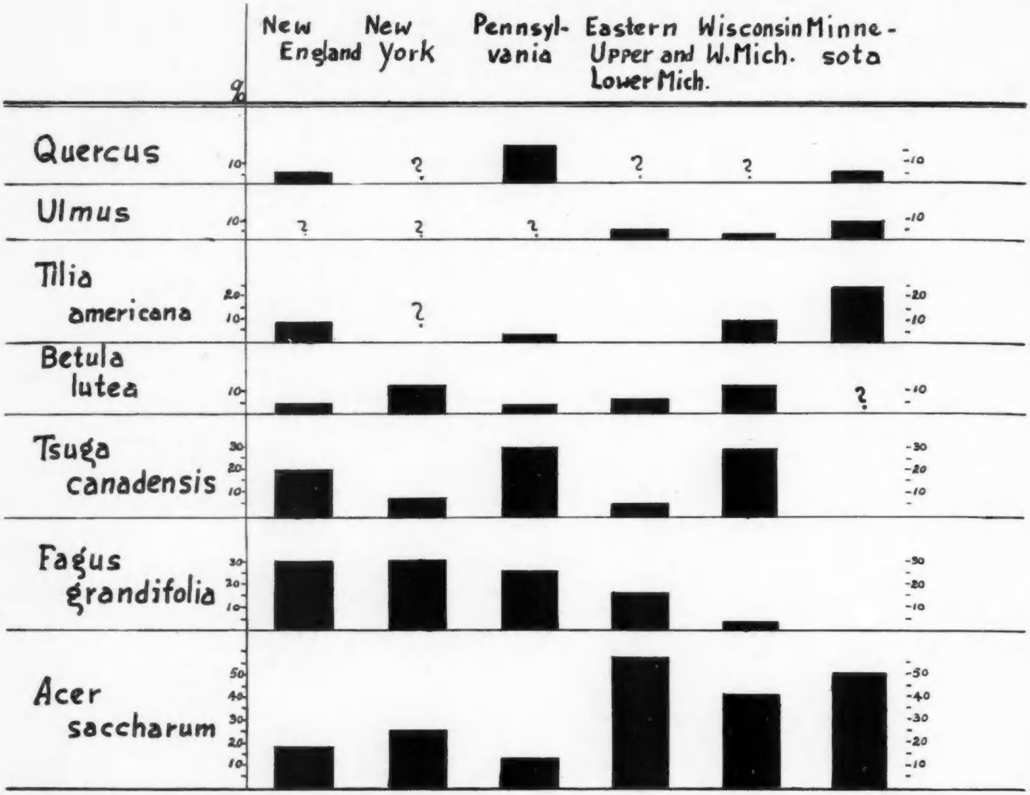


FIG. 31. Graphic presentation of differences in abundance of climax forest associates in an east-west transect of the lake forest. Averaged quantitative reports for a given region were used as basis of the percentage figures.

LITERATURE CITED

Adams, C. C. 1902. Postglacial origin and migration of the life of northeastern United States. Jour. Geog. **1:** 303-310, 352-357.

Alway, F. J., & P. R. McMiller. 1933. Interrelationships between soil and forest cover on Star Island, Minnesota. Soil Sci. **36:** 281-294.

Bergman, H. F. 1923. The composition of climax plant formations in Minnesota. Mich. Acad. Sci., Arts, and Letters, Papers **3:** 51-60.

Brown, C. A. 1938. The flora of Pleistocene deposits in the western Florida Parishes; West Feliciana Parish, East Baton Rouge Parish, Louisiana. Dept. Conserv. La. Geol. Surv., Geol. Bul. 12.

Buell, Murray F., & William E. Gordon. 1945. Hardwood-conifer forest contact zone in Itasca Park, Minnesota. Amer. Midl. Nat. **34:** 433-439.

Buttrick, P. L. 1923. Second growth hardwood forest in Michigan. Mich. Agr. Coll. Special Bul. **123.**

Cain, Stanley A. 1939. The climax and its complexities. Amer. Midl. Nat. **21:** 146-181.

1944. Foundations of Plant Geography. Harper & Bros. New York.

1945. The place of pollen analysis in Paleoecology. Chronica Bot. **9:** 106-114.

Clayberg, H. D. 1920. Upland plant societies of Petoskey-Walloon Lake region. Bot. Gaz. **69:** 28-53.

Cooper, W. S. 1913. The climax forest of Isle Royale, Lake Superior and its development. Bot. Gaz. **55:** 1-44, 115-140, 189-235.

Cooper, W. S. 1942. Vegetation of the Prince William Sound region, Alaska; with a brief excursion into post-Pleistocene climatic history. Ecol. Monog. **12:** 1-22.

Conard, Henry S. 1939. Plant associations on land. Amer. Midl. Nat. **21:** 1-27.

Cunningham, R. W., & H. G. White. 1941. Forest resources of the Upper Peninsula of Michigan. U. S. Dept. Agr. Miscl. Pub. **429.**

Dachnowski, Alfred P. 1921. Peat deposits and their evidence of climatic changes. Bot. Gaz. **72:** 57-89.

Dansereau, Pierre. 1944. Interpenetrating climaxes in Quebec. Sci. **99:** 426-427.

Daubenmire, Rexford F. 1931. Factors favoring the persistence of a relic association of eastern hemlock in Indiana. Butler Univ. Bot. Stud. **2:** 29-32.

1936. The Big Woods of Minnesota; its structure and relation to climate, fire and soils. Ecol. Monog. **6**: 233-268.

Deevey, Edward S., Jr. 1943. Additional pollen analyses from southern New England. Am. Jour. Sci. **241**: 717-752.

Duerr, William A., & Charles H. Stoddard, Jr. 1938. Results of a commercial selective cutting in a northern hemlock-hardwoods. Jour. Forestry **36**: 1224-1230.

Friesner, Ray C., & J. E. Potzger. 1932. Studies in forest ecology II. The ecological significance of Tsuga canadensis in Indiana. Butler Univ. Bot. Stud. **2**: 144-150.

1934. Climax conditions and the ecological status of Pinus strobus, Taxus canadensis, and Tsuga canadensis in the Pine Hills region of Indiana. Butler Univ. Bot. Stud. **3**: 65-84.

Frothingham, E. H. 1915. The northern hardwoods forest: its composition, growth and management. U. S. Dept. Agr. Bul. **285.**

Gates, F. C. 1917. The relation between evaporation and plant succession in a given area. Amer. Jour. Bot. **4**: 161-178.

1926. Plant succession about Douglas Lake, Cheboygan County, Michigan. Bot. Gaz. **82**: 170-182.

1942. The bogs of northern lower Michigan. Ecol. Monog. **12**: 213-254.

Gleason, H. A. 1923. The vegetational history of the Middle West. Assoc. Amer. Geog., Ann. **12**: 39-85.

1924. The structure of the maple-beech association in northern Michigan. Mich. Acad. Sci., Arts, and Letters, Papers **4**: 285-296.

1939. The individualistic concept of the plant association. Amer. Midl. Nat. **21**: 92-110.

Grant, H. M. 1934. The climax forest community in Itasca County, Minnesota and its bearing upon the successional status of the pine community. Ecology **15**: 243-257.

Griggs, Robert F. 1934. The edge of the forest in Alaska and the reasons for its position. Ecology **15**: 80-96.

Halliday, W. E. D., & A. W. A. Brown. 1943. The distribution of some important forest trees in Canada. Ecology **24**: 353-373.

Harshberger, John W. 1911. Phytogeographic survey of North America. G. E. Stechert & Co. New York.

Harvey, Leroy H. 1920. Some phytogeographical observations in Lake County, Michigan. Mich. Acad. Sci., Rept. **21**: 213-217.

Howell, John W. 1938. A fossil pollen study of Kokomo Bog, Howard County, Indiana. Butler Univ. Bot. Stud. **4**: 117-127.

Jennings, O. E. 1909. A botanical survey of Presque Isle, Erie County, Pennsylvania. Carnegie Mus. Ann. **5**: 289-421.

Kell, Lucille Lora. 1938. The effect of moisture-retaining capacity of soils on forest succession in Itasca Park, Minnesota. Amer. Midl. Nat. **20**: 682-694.

Keller, Carl O. 1943. A comparative study of three Indiana bogs. Butler Univ. Bot. Stud. **6**: 65-80.

Kenoyer, Leslie A. 1930. Ecological notes on Kalamazoo County, Michigan, based on original land survey. Mich. Acad. Sci., Arts, and Letters, Papers **11**: 211-217.

1934. Forest distribution in southwestern Michigan as interpreted from the original land survey (1826-1832). Mich. Acad. Sci., Arts, and Letters, Papers **19**: 107-111.

Kittredge, J. 1934. Evidence of the rate of forest succession on Star Island, Minnesota. Ecology **15**: 24-35.

Leopold, Aldo. 1943. Deer irruptions. Wis. Acad. Sci., Arts, and Letters, Trans. **35**: 351-366.

Lindsey, Alva. 1932. The Merrillville white pine bog in Lake County, Indiana. Butler Univ. Bot. Stud. **2**: 167-178.

Livingston, B. E. 1903. The distribution of the upland plant societies of Kent County, Michigan. Bot. Gaz. **35**: 36-55.

1905. The relation of soils to natural vegetation in Roscommon and Crawford counties, Michigan. Bot. Gaz. **39**: 22-41.

Lutz, Harold J. 1928. Trends and silvicultural significance of upland forest successions in southern New England. Yale Univ., School Forestry Bul. **22.**

1930. The vegetation of Hearts Content, a virgin forest in northwestern Pennsylvania. Ecology **11**: 1-29.

1930. Original forest composition in northwestern Pennsylvania as indicated by early land survey notes. Jour. Forestry **28**: 1098-1103.

Maissurow, D. K. 1941. The role of fire in perpetuation of virgin forests of northern Wisconsin. Jour. Forestry **39**: 201-207.

Marks, John B. 1942. Land use and plant succession in Coon Valley, Wisconsin. Ecol. Monog. **12**: 113-133.

McCarthy, Edward F., & Harold Cahill Belyea. 1920. Yellow birch and its relation to the Adirondack forest. New York State Coll. Forestry Tech. Publ. **12.**

McIntyre, G. S. 1931. Theory and practice of forest typing with special relation to the hardwood and hemlock associations of northern Michigan. Mich. Acad. Sci., Arts, and Letters, Papers **15**: 239-251.

Merrill, Perry H., & Ralph C. Hawley. 1924. Hemlock: Its place in the silviculture of the southern New England forest. Yale Univ., School Forestry Bul. **12.**

Nichols, G. E. 1935. The hemlock-white pine-northern hardwoods region of eastern North America. Ecology **16**: 403-422.

Otto, James H. 1938. Forest succession in the southern limits of Early Wisconsin glaciation as indicated by a pollen spectrum from Bacons Swamp, Marion County, Indiana. Butler Univ. Bot. Stud. **4**: 93-116.

Potzger, J. E. 1935. Topography and forest types in a central Indiana region. Amer. Midl. Nat. **16**: 212-229.

1939. Microclimate and a notable case of its influence on a ridge in central Indiana. Ecology **20**: 29-37.

1941. The vegetation of Mackinac Island, Michigan: An ecological survey. Amer. Midl. Nat. **25**: 298-323.

1942. Pollen spectra from four bogs on the Gillen Nature Reserve along the Michigan-Wisconsin state line. Amer. Midl. Nat. **28**: 501-511.

1943. Pollen profile from sediments of an extinct lake in Hendricks County, Indiana marks time of drainage. Indiana Acad. Sci. Proc. **52**: 83-86.

1943. Pollen study of five bogs in Price and Sawyer counties, Wisconsin. Butler Univ. Bot. Stud. **6**: 50-64.

1944. The vegetation of Round Island (Straits of Mackinac), Michigan. Butler Univ. Bot. Stud. **6:** 116-121.

1945. The Pine Barrens of New Jersey, a refugium during Pleistocene times. Butler Univ. Bot. Stud. **7:** 182-196.

1946. A pollen study along the tension zone of the lake forest in Lower Michigan. (MS.)

Potzger, J. E., & Ray C. Friesner. 1939. Plant migration in the southern limits of Wisconsin glaciation in Indiana. Amer. Midl. Nat. **22:** 351-368.

1940. What is climax in Central Indiana? A five-mile quadrat study. Butler Univ. Bot. Stud. **4:** 181-195.

Potzger, J. E., & Carl O. Keller. 1944. A pollen study of four bogs along the southern border of Vilas County, Wisconsin. Wis. Acad. Sci., Arts, and Letters, Trans. **35:** 147-156.

Potzger, J. E., & James H. Otto. 1943. Post-glacial forest succession in northern New Jersey as shown by pollen records from five bogs. Amer. Jour. Botany **30:** 83-89.

Potzger, J. E., & Ruth R. Richards. 1942. Forest succession in the Trout Lake, Vilas County, Wisconsin area: A pollen study. Butler Univ. Bot. Stud. **5:** 179-189.

Potzger, J. E., & B. C. Tharp. 1943. Pollen record of Canadian spruce and fir from Texas bog. Sci. **98:** 584-585.

Potzger, J. E., & Ira T. Wilson. 1941. Post-Pleistocene forest migration as indicated by sediments from three deep inland lakes. Amer. Midl. Nat. **25:** 270-289.

Quick, B. E. 1923. A comparative study of the distribution of the climax association in southern Michigan. Mich. Acad. Sci., Arts, and Letters, Papers **3:** 211-244.

Raup, Hugh M. 1941. Botanical problems in Boreal America. Bot. Rev. **7:** 147-248.

Rosendahl, C. O., & F. K. Butters. 1928. Trees and Shrubs of Minnesota. Univ. Minn. Press.

Sears, Paul B. 1942. Postglacial migration of five forest genera. Am. Jour. Bot. **29:** 684-691.

Shirley, Hardy L. 1941. Restoring conifers to aspen lands in the Lakes States. U. S. Dept. Agr., Tech. Bul. **763.**

Smith, Lloyd F. 1940. Factors controlling the early development and survival of eastern white pine in central New England. Ecol. Monog. **10:** 373-420.

Stallard, Harvey. 1929. Secondary succession in the climax forest formation of northern Minnesota. Ecology **10:** 476-547.

Taylor, Norman. 1928. The vegetation of the Allegheny State Park. Univ. State of N. Y., State Museum Handbook **5.**

Transeau, E. N. 1903. On the geographic distribution and ecological relations of the bog plant societies of northern North America. Bot. Gaz. **36:** 401-420.

Turesson, G. 1929. Zur Natur und Begrenzung der Arteinheiten. Hereditas **13:** 177-184.

Weaver, John E., & Frederic E. Clements. 1938. Plant Ecology. McGraw-Hill Book Company, Inc. New York.

Welch, Winona H. 1936. Boreal relics in Indiana. Indiana Acad. Sci. Proc. **45:** 78-88.

Westveld, R. H. 1933. Relation of certain soil characteristics to forest growth and composition in the northern hardwood forest of northern Michigan. Mich. State College Agr. Expt. Sta., Tech. Bul. **135.**

Whitford, H. N. 1901. The genetic development of the forests of northern Michigan: A study in physiographic ecology. Bot. Gaz. **31:** 289-325.

Wilson, Ira T. 1941. A new device for sampling lake sediments. Jour. Sed. Petrology **11:** 73-79.

Wilson, Ira T., & J. E. Potzger. 1943. Pollen study of sediments from Douglas Lake, Cheboygan County and Middle Fish Lake, Montmorency County, Michigan. Indiana Acad. Sci. Proc. **52:** 87-92.

1943. Pollen records from lakes in Anoka County, Minnesota: A study on methods of sampling. Ecology **24:** 382-392.

Young, Vernon A. 1934. Plant distribution as influenced by soil heterogeneity in Cranberry Lake region of the Adirondack Mountains. Ecology **15:** 154-196.

Zon, Raphael, & H. F. Scholz. 1929. How fast do northern hardwoods grow? Univ. Wis. Agr. Expt. Sta. Research Bul. **88.**